The Black-footed Ferret

EDSON FICHTER

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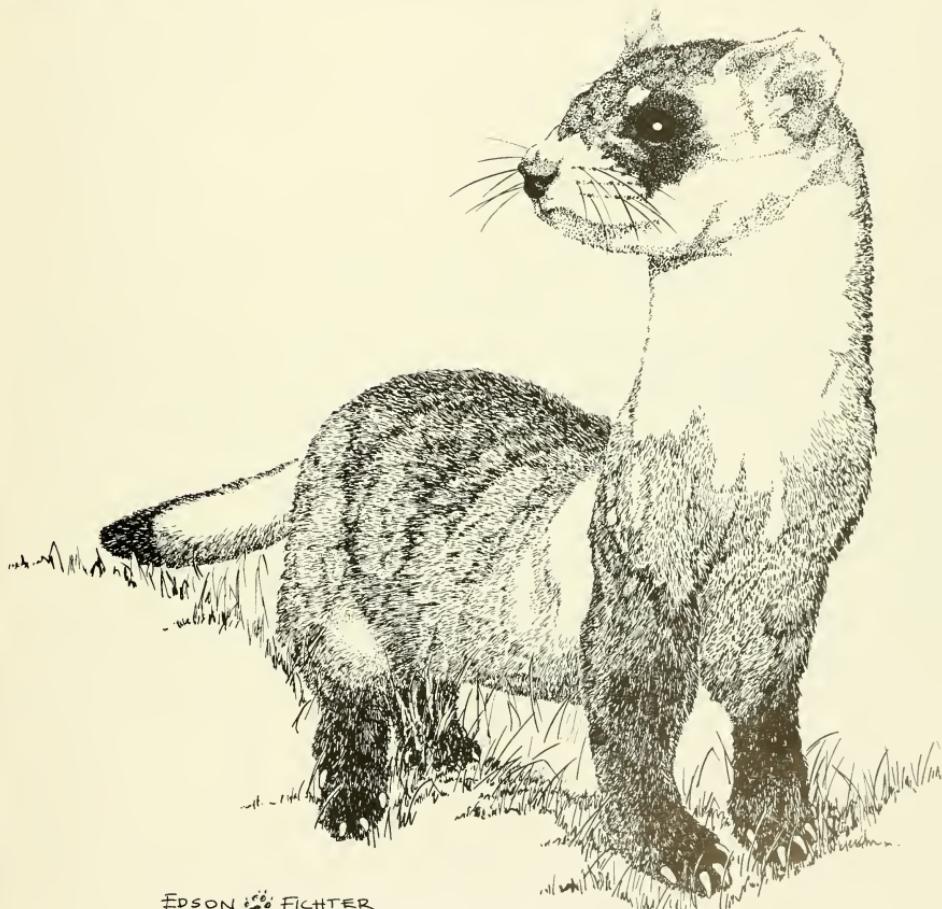
INTRODUCTION

Archie Carr III[1]

ABSTRACT.—Context for the Meeteetse, Wyoming, black-footed ferret studies and recovery efforts, reported in this volume, is presented.

This is the second draft of this manuscript. My first draft was ready in the early summer of 1985. It conveyed a sense of confidence about the survival prospects of the black-footed ferret, *Mustela nigripes*. By the fall of the year at press time, circumstances had changed so dramatically that draft 1 became obsolete and the editor asked for a rewrite. I submit draft 2 with dismay and no sense of what the future holds. As for the ferrets, 6 are in captivity in a place called Sybille Canyon in Wyoming; perhaps 10 are still out there near Meeteetse, in a sprawling prairie dog colony in the Big Horn Basin of northwestern Wyoming; canine distemper has swept the ferrets; plague has been confirmed in the prairie dogs; and options for management have dwindled like Custer's Last Stand.

As a result, I write from unsure footing. The series of papers contained herein were intended to report on the natural history and management criteria of a critically endangered species, the black-footed ferret, and to highlight data that might contribute to its recovery. The research, and publication here of the results, seemed to be two steps in an orderly, modern, even scientific, recovery process. This introduction addresses that "process," endeavoring to record the perplexing political events that occurred concurrently with the field research following the ferret's rediscovery in 1981; events that by

late 1985 have left an unnecessarily critical and unpromising survival outlook for the species; events that may have made an epitaph of this monograph.

The ferret is a legal animal. By virtue of the U.S. Endangered Species Act the ferret enjoys something akin to "standing." It cannot be legally abused or ignored. That is the beauty, the novelty, of the act. Thus, when a species enjoying that novel standing is seen to decline, one must question the fitness of the act itself. That is not to say that one can take the ESA for granted as a tool for species survival. On the contrary, this act, like other federal laws, has always taught a strict lesson in civics: democracy is what you make of it.

No major social advance since World War II has intrigued me more than the Endangered Species Act of 1966. I was young when the act was passed. My generation was idealistic in those days. The act restored the conservationist's faith in America as a rational society and in government as a body capable of responding to the will of the people. The Endangered Species Act, coming as it did after the orgy of materialism during the previous decade, affirmed that the general public was ready to acknowledge that, aside from tangible wealth, prosperity meant preserving the natural heritage of the country. Government would be the willing vehicle of this philosophical renaissance.

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The act has matured since then, and so have I. When the act was passed I supposed that species were saved and that I could devote my own energies to other matters. In the intervening years, years of tremendous social challenges in the U.S., ranging from civil rights to Vietnam, I gradually gained insight on a concept I came to call "ghost government." The reality is that no matter how fine a governmental system may be, the citizen should expect little from it if he or she is unwilling to be involved in its operation—forever. Ghost governance. As in ghost writing. A governmental system is only as successful as the ghost government of citizens that watches it and coddles it and intimidates it and pats it on the back. It would seem to be an inefficient process, but it works, and the crucial thing about a democracy is that it permits this ghost government, this band of sometimes unruly interest groups, to participate freely in the stewardship of society—and black-footed ferrets.

Plainly my thesis is that a congressional mandate to a government agency has been an inadequate incentive to save the ferret. The mandate to save this animal is clearly there in the Endangered Species Act. But implementing that mandate has required a frustrating but persistent give-and-take between citizens and the mandated agencies. Ghosting.

If the hand-holding role of the citizenry was at all unusual in 1981 in mobilizing government to respond to the ferret's plight, it was made necessary, in part, by the unusual times of the ferret. One must recall that immediately before the ferret's rediscovery came the appointment of James Watt as Secretary of the Interior. The anti-act posture of this secretary demoralized federal officers and damaged budgets to such an extent that no real government rally to help the ferret ever arose. The ferret was given no significant "priority." The ghost government responded in two ways: first, it tried to foster its own rally, and I'll discuss that more below. Secondly, it "dumped" James Watt. Democracy is what you make of it.

With the exception of James Watt, the individuals involved in the early acts of the ferret's saga were more captivating than the agencies. That's perhaps the way it is most often with "issues" in American life. Individuals make things happen. One figure who intrigues me

in particular is Mr. Jack Turnell, manager of the Pitchfork Ranch, where most of the remnants of the only known ferret colony existed. I have yet to meet Mr. Turnell, but I think he is a national hero. He made certain decisions shortly after the ferrets were found that, frankly, assured them a chance for recovery. My guess is that Turnell made these decisions out of some personal conviction about wildlife and the West and humanity's obligations to the world we live in. His direct interest in the ferret was crucial because, as I have said, governmental authorities were not moving with alacrity at the time. So, Mr. Turnell fascinates me. Someday perhaps I'll have the chance to talk to him about those early days, and the sacrifices to his land and privacy that he perceived to be concomitant with helping a federally protected species. There are few people in history who have had the opportunity and the power to unilaterally decide to save a species.

A second prominent figure in modern ferret lore is Dr. Tim Clark who, it is fair to say, owes much of his notoriety to Jack Turnell. One of the crucial decisions Turnell made was to agree to let Tim Clark look for and study the ferrets on the ranch. I have had the privilege of knowing Dr. Clark. He is not a boastful fellow, but surely he deserves no less a title than "Mr. Ferret." In support of the claim I need only refer to the authorship of many of the manuscripts that follow. Tim's interests know no bounds when it comes to black-footed ferrets. He has done the hard field research; he has publicized the plight of the ferret; he has lobbied; and he has raised money.

In keeping with his predilection for holistic research, Tim also took an academic interest in the dynamics of American conservation, as represented by the unfolding story of the ferret. My own organization, Wildlife Conservation International, was scrutinized in this regard.

Wildlife Conservation International (WiCI), the division of the New York Zoological Society (NYZS) that concerns itself with field conservation, is chiefly devoted to work outside the United States, mostly in the tropics. This emphasis is based on the observation that the United States is amply endowed with conservation agencies and conservation money, es-

Fig. 1. This 1906 photograph is believed to be the first one taken of a black-footed ferret (New York Zoological Society photo).

pecially when compared to the species-rich countries of the developing world. In the United States, an endangered species might expect attention from layers of interested parties: the federal government, state government, private nongovernmental organizations including universities, and, of course, indi- viduals. Such infrastructure is rarely present in the Third World, and so WiCI concentrates its efforts there, conducting and supporting research on the biology of endangered spe- cies. We call it conservation biology, and, at any given moment, we will have 30 or so projects underway.

However, since the founding of NYZS in 1895, the society has never entirely divorced itself from species conservation in the United States. In the early part of this century, the vociferous contributions of William Horna- day, the first director of NYZS, to shaping the U.S. Fish and Wildlife Service, its refuge sys- tem, and the early laws entrusted to it suc- ceeded in leaving a permanent NYZS imprint on American wildlife conservation. The soci- ety also takes considerable pride in having played a central role in restoring the Ameri- can bison to the western plains between 1905 and 1919. In conjunction with the federal gov- ernment, remnant groups of bison were gath- ered at the society's Bronx Zoo, in New York.

Stocks from the combined herd were sent by rail to such protected areas as the Wichita Mountains Wildlife Refuge.

Among the studies sponsored by NYZS in this country is one of particular relevance to the present monograph. It is Carl Koford's work with prairie dogs, appearing in 1958 as "Prairie Dogs, White Faces and Blue Grama" in the journal *Wildlife Monographs*. Koford's was the first major technical paper to show a tie between prairie dog eradication and ferret decline. It was a deadly tie indeed.

The society was helpful to Koford's pre- scient research and now finds itself back in the West, again with the ferrets, this time pro- moting science appropriate to recovery. De- spite our current commitment to conservation biology abroad, the society's affection for wildlife of the West is clear. In fact the attach- ment is symbolized in the logo of NYZS, a bust of the bighorn sheep.

In the fall of 1981 the U.S. Fish and Wildlife Service's *Endangered Species Technical Bul- letin* announced the discovery of a black- footed ferret colony near Meeteetse, Wyo- ming. It was electrifying news, and a host of American conservation groups perked up, looking for ways to lend a hand. Just about every one had accepted the USFWS bitter decision three years prior to consider the fer-

ret extinct. Everyone, that is, except for a very few individuals who kept searching throughout those bleak years.

A shaggy ranch dog turned things around. It's true, the dog killed the only ferret anyone had seen in years, but the single specimen, probably a wayfaring yearling from the colony, was tangible evidence that a whole species still lived.

I confess, I don't mind defending the dog. I met him once. His name is Shep. He is very tractable, and blithely unconcerned with the hoopla stirred up by his routine vigilance.

Following the *Bulletin's* report of the ferret find, Wildlife Conservation International made the decision to become involved in the species' recovery. We were influenced by three considerations:

1. Without doubt—and without apology— we saw public-relations value in taking a leadership role in the potential restoration of this highly publicized American species. A good job with the little ferret would help us in the chronic task of raising funds for other species. The ferret might have become a mini-panda, valuable to our image making. And so, we dominated the private funding picture from 1982 to 1985.

2. Secondly, there was the political situation, to which I have alluded before. In the view of most conservationists in late 1981, the Endangered Species Act was in jeopardy, and consequently the ability of the federal government to respond constructively to the ferret find was predicted to be limited. The times were chaotic for wildlife conservation. Already that autumn I had joined a letter-writing campaign to halt dismantling of USFWS Cooperative Wildlife Research Units at universities all over the country. The Endangered Species Office budget had been slashed. The secretary of interior had declared that his department would list no more endangered species, just as it would gazette no new national parks. It was a tough time to arise from the dust of extinction, and we at WiCI felt that if we didn't make a move to help the ferret, the little beast might actually slip back into oblivion. It's expected savior, Uncle Sam, was hobbled by an anomalous secretary of the interior.

3) Our third motivation for entering ferret history was a practical one. After reading the first reports that the ferret colony might consist of a couple of dozen breeding animals, we were very certain that captive breeding and establishment of new colonies would be recommended. That form of animal management has attained a high degree of sophistication at the Bronx Zoo, the sister organization to WiCI in the New York Zoological Society. The cadre of NYZS people involved in captive breeding of wildlife, from curators to veterinarians, is large and skilled, and we planned to make it clear to all concerned that we were ready to contribute when the time came.

With these circumstances in mind, we set about to find an outlet for our good will, talent, and cash. At precisely the same moment, one Dr. Tim Clark began inquiring of possible WiCI interest in granting support for his fer ret studies. His field work—counts, feeding behavior, reproduction studies—were precisely the type of biology favored by WiCI, and his commitment to working in conjunction with the complex federal-state mechanism reassured us that our sponsorship would go toward an influential project. We began work with Tim Clark and his Biota Research and Consulting, Inc. in 1982.

Largely through Dr. Clark's initiatives, the ferrets attracted the attention of numerous other conservation organizations, most of whom assisted Clark's project directly. These included the World Wildlife Fund—U.S., the National Geographic Society, the National Wildlife Federation, and the Charles A. Lindbergh Fund. Aside from contributing cash, several of these prominent nongovernmental organizations assumed lobbying tasks in Washington in support of the ferret. But Dr. Clark's first support—given even before the ferrets were discovered, and sustained, one presumes, out of blind faith that some animals must have remained somewhere in the vastness of the West—came from the little-known Wildlife Preservation Trust International (WPTI). WPTI is an American-based offshoot of the Jersey Wildlife Preservation Trust, an institution given prominence by Gerald Durrell, director of the famous Jersey Zoo in England.

A discernible recovery program began to take shape in Wyoming. The one known colony was secured, thanks in large part to the unusual cooperation of the owners of the only

inhabited ferret land. Research was begun promptly and was pursued with vigor, to the extent that, as the papers contained herein and others reveal, we quickly learned the size of the single colony, its demographics, and that possibly "surplus" youngsters were available every fall as potential candidates for captive breeding or translocation. We learned how to search for ferrets, and, tragically, that over tremendous areas of potential habitat there were no more ferrets. The American conservation community rallied effectively to underwrite the bulk of the research to the tune, cumulatively, of over $550,000, according to a recent manuscript by Tim Clark. In the final analysis, cooperation in the field between government and nongovernmental agencies was satisfactory. To help enhance this atmosphere of cooperation, the Black-footed Ferret Advisory Team (BFAT) was put together, a sort of clearing house for the growing interest in black-footed ferrets.

I became optimistic. I thought I sensed a surge of enthusiasm among ferret people, a threshold of determination that, once crossed, would overwhelm whatever obstacles might be thrown up by the Watt administration.

In April 1982 I saw a ferret and was inspired even more. I flew out to Cody, Wyoming, with Jim Doherty, the seasoned curator of mammals for the New York Zoological Society. I was anxious for Jim to accompany me because already we were certain that captive breeding of ferrets would become a recovery priority, and Jim could represent the society's expertise in this field.

We drove south to Meeteetse and joined Tim Clark and his research associates Tom Campbell, Louise Richardson, and Steve Forrest. They were the principal figures in the field program and they introduced us to the research. Later I wrote about the outing in our newsletter, *the Ferret*, first published shortly after WiCI joined forces with Tim and his colleagues:

After a day with Tim Clark, exploring the prairie dog colony where the ferrets clung to their tenuous future, . . . Jim Doherty and I joined ferret biologist Tom Campbell for a unique adventure. Driving in a pickup truck along a graded road near the prairie dogs in the dead of night, we saw a black-footed ferret. We were lucky.

Only nine individuals had been found by spotlighting since Clark and Campbell had begun their surveys back before Christmas. Our ferret came bounding across the prairie in its odd, accelerated inch-worm gait and wound up in a prairie dog den twenty feet from the right fender of the truck. We feasted on the view for many excited minutes.

The ferret was as high strung and energetic a creature as I had ever seen. It fairly crackled with nervous impulses, first digging, then stretching to stare, then circling the den, then looping back in. I was moved by the idea that if we humans would give the ferret half a chance, that purposeful dynamo would surely do the rest.

It was a nice sentiment at the time. It seems naive now, because that "half a chance" was never granted.

Time passed. The field work continued. Searches for ferrets were begun in other states. Litters of ferrets were recorded at Meeteetse. Data were published. Letters were written. No progress was made toward captive breeding during 1982 and 1983.

Finally, at the request of the nongovernmental conservation community, a meeting was called by the Wyoming Game and Fish Department in the spring of 1984 in Cheyenne. Jim Doherty and I were invited to participate. The meeting would include field biologists, veterinarians, and administrators representing federal, state, and private agencies, essentially the extended network of people responsible for the survival of the black-footed ferret.

Sure enough, captive management became the focus of the meeting just as soon as the introductory material was set aside. Tim Clark and his colleagues presented enough demographic data to suggest that the Meeteetse ferret colony was stable or even growing. Arriving at comparable figures from year to year is difficult because census methods were evolving and improving as time went by, but the best published estimates for all years, based on early August counts of adults and young, are as follows:

1982	61 (incomplete survey)
1983	88
After this meeting:	
1984	129
1985	58

The 1983 figure and the abundance of youngsters every fall relative to the number of adults, were strong indications that ferrets

could be captured without jeopardizing the Meeteetse colony. Thinking back to that large gathering in Cheyenne, I recall a universal consensus that establishment of one or more captive colonies was of utmost urgency. The chief justifications were (a) to provide a strategic cushion in the event a disease—an epizootic—struck the little Meeteetse population and (b) to provide, in the course of time, the stock for recolonization of suitable ferret habitat. It was sound, if belated, reasoning. The only dissention came in deciding how to do it.

As early as 1981 the U.S. Fish and Wildlife Service had granted Wyoming Game and Fish Department "lead agency" status for ferret recovery, a legal courtesy permitted under the Endangered Species Act. Thus, Wyoming Game and Fish had begun to organize activities, helping foster BFAT, convening the Cheyenne meeting, and generally assuming responsibility for major decisions. Assumption of leadership by a state agency in this manner had precedent elsewhere; and, in cases where the federally protected species is limited in distribution, it seems a logical way to implement the act. Provided the surrogate agency responds to the federal mandate, the process is viable.

At Cheyenne we began to see the hang-up on captive breeding as an element in the survival process. State officials, while concurring with the captive propagation tactic, an- nounced firmly that no ferrets would leave Wyoming to achieve this purpose. Simultaneously they declared that their own Sybille Canyon Wildlife Research Unit was unsatisfactory as a captive breeding facility, an ironic viewpoint as things turned out; and they concluded that federal and/or private agencies should pay for the cost of building and staffing a proper facility in Wyoming.

In view of the availability of well-equipped, well-staffed, well-funded facilities in several locations around the U.S., this pronouncement by the lead agency for ferret recovery was met with consternation by both federal and private nonprofit organization representatives. The 1984 capture season (September-October, when young of the year are weaned and dispersing) came and went, but the Cheyenne impasse prevailed despite the probabilistic certainty of the consequences.

In May of 1985 a decision was made by state and federal officers to attempt to capture ferrets in October, provided the scheduled summer counts showed an acceptable but unspecified surplus. Sybille Canyon was agreed upon as a holding facility, but no specific breeding facility was identified. Almost concurrently with the meeting, plague was reported among the white-tailed prairie dogs of Meeteetse, the prey base of the ferrets. To everyone's relief, the mustelids, evidently, were immune to plague, but there loomed the possibility of starvation for ferrets if the prairie dog die-back was too severe. As it turned out, the plague episode served chiefly as an unnerving object lesson of the principles of epizootic disease, principles that were familiar to most of us from the beginning.

During the period June-October 1985, the principles were applying themselves with mortal vigor. The July-August count gave strong indications that something was amiss, but no real credence was given the declining population figures until 22 October. By that time supplementary surveys in September had arrived at a count of 31 ferrets, one month after the August estimate of 58, and by October 9 only 13 ferrets were seen in the field.

Six ferrets had been captured by early October and brought to the Sybille Canyon Wildlife Research Unit. On 22 October one of these animals was reported dead and the cause was diagnosed as canine distemper. Wyoming Game and Fish acknowledged that the disease was "probably the worst event that could have occurred in the ferret population."

Immediately a capture team was sent to the field to capture as many of the threatened remaining ferrets as possible. Six were brought in by the following week when the capture term was withdrawn before capturing all the ferrets. Biologists departing the scene after the emergency exercise guessed that fewer than 10 remained in the Meeteetse population. Their significance to the future of the species must be regarded as negligible for the time being. Their numbers are few; they are scattered over a vast terrain; distemper is presumably still among them; and the Wyoming winter is coming on.

Now, after additional deaths in the captive group, six ferrets remain. The Sybille Six. There is no cushion. For a while the best of

American wildlife science might have governed the future of this species. Now luck is the guiding force. We need luck with the Sybille Six, that they might multiply; and we need luck out on the prairies, that some stalwart surveyor might chance upon yet another last colony of black-footed ferrets.

The black-footed ferret once enjoyed a range about as extensive as any that North America can offer, encompassing all of what we call the Great Plains and beyond. The little mustelid was the incidental victim of one of the most diligent vertebrate pest control exercises in history: the attempt to eradicate prairie dogs for the alleged benefit of livestock grazing. The assault changed prairie dog distribution dramatically. In the process it wiped out ferrets from Canada to Mexico—except for the few discovered near Meeteetse.

History should record that rational people stepped forward when the Meeteetse colony was found. Among them were the authors of the papers that follow, people who assumed

that they worked within a rational system, far different from the cavalier times that brought the ferret so near extinction in the first place. But that system, ultimately based in the U.S. Endangered Species Act, has failed the ferret. It had converted a tense but hopeful outlook for the species into a crisis. The system became impotent as decision makers locked themselves into years of indecision as to the venue for captive propagation of ferrets.

Altogether, the species has not fared well in its ecological partnership with modern man. But in every such sad story there is a lesson. The ferret story may contain two. Following its first decline, we people reviewed our use of pesticides, our fanatical reaction to agricultural "pests," our obligation to public lands; and our general management of Great Plains land, whether private or public. I believe the message of the ferret's second decrement is that the U.S. Endangered Species Act may no longer be the safety net for American wildlife that Congress intended it to be.

TECHNICAL INTRODUCTION

Tim W. Clark[1]

ABSTRACT.—The contents of this volume and their relationship to ferret conservation and recovery are discussed.

The critically endangered black-footed fer ret (*Mustela nigripes*) has been an enigma ever since its scientific discovery in 1851 by John James Audubon and John Bachman. In 1877 Dr. Elliott Coues of the Smithsonian Institution reported that the ferret was com mon to the plains of the West and associated with prairie dogs (*Cynomys* sp.). Collection records show that, until the first decades of this century, ferrets were distributed over about 40 million ha in 12 states and 2 Canadian provinces. By the late 1940s, no ferrets could be located for study, ostensibly because of a precipitous decline in population size and dis tribution, from habitat loss (the poisoning of prairie dogs), and perhaps other factors. The ferret was considered extinct or nearly so when in 1964 a small population was discov ered in South Dakota and the species came under study for the first time—113 years after its scientific discovery.

Three chapters stand out in ferret study and conservation: (1) From the 1830s to 1964, dur ing which time specimens were occasionally collected and a few natural history observa tions recorded; (2) from 1964 to 1981, when the Mellette County, South Dakota, ferret population was discovered and studied for 11 years (ca 90 different ferrets were observed, including 11 litters) and it dwindled to extinc tion. Attempts to breed a few ferrets in captiv ity came too late, and no other populations were discovered despite surveys. Many peo ple feared the ferret was extinct; (3) from 1981 to date, when the Meeteetse, Wyoming, fer ret population was discovered and studied (ca 129 different ferrets were seen, including 25 litters in 1984). In part, this period closes with this volume and the many other conservation biology papers resulting from the Meeteetse studies (see Casey et al. in this monograph). All these papers describe key aspects of the Meeteetse ferret population, habitat require ments, and means of managing and recover ing the species. We hope this third chapter will usher in a fourth chapter—full recovery of the species to secure, viable populations scattered over portions of its former range.

Individually and collectively, the 14 original contributions to this monograph, plus the in troductory remarks by Dr. Archie Carr III, provide a much fuller understanding of the spe cies and the foundation needed for full species recovery. Other study results on the Meeteetse ferrets have been published elsewhere, and they, too, add significantly to our understanding of the ferret and its conservation needs. To be sure, many details about ferret behavior and ecology remain to be learned, but they can wait until the ferret is more common and can accom modate rigorous scientific scrutiny in laboratory and field. These 14 papers describe numerous aspects of ferret biology, management, and re covery direction—all for the first time.

First, Anderson et al. examine the ferret's fossil record as well as recent distribution and systematics. Pleistocene and Holocene faunas $(n=21)$ show ferret remains. Ferret distribu tion based on 412 specimens in 68 museums from Arizona, Colorado, Kansas, Montana, Nebraska, New Mexico, North Dakota, Okla homa, South Dakota, Texas, Utah, Wyoming, and Canada are summarized. Comparisons of Pleistocene with Recent specimens show no significant differences in size or morphology. Analysis suggests no consistent morphometric variation exists between ferrets found in asso ciation with different prairie dog species.

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The second section comprises five contributions dealing with ferret habitat—historic habitat, the status and characteristics of the Meeteetse area, and methods for locating and measuring potential habitat for reintroductions. The Flath and Clark paper gives a description of ferret habitat—prairie dogs— prior to large-scale alteration of the landscape by early Montana settlers. Their paper describes prairie dog distributions between 1908 and 1914, just prior to the 1915 U.S. Biological Survey efforts to destroy the prairie dog. It shows extensive prairie dog colonies, which today have been nearly eliminated (90+%). It is clear that habitat loss is the single most significant factor in ferret endangerment. The next paper by Clark et al. gives a description and history of the Meeteetse ferret environment. It shows that ferrets have occurred in the region for at least 100 years.

Currently ferrets occupy about 2,995 ha of white-tailed prairie dog (*C. leucurus*) colonies that are owned in equal portions by private, state, and federal interests. Many abandoned prairie dog colonies in the immediate area, scattered over large cattle ranches, along with the currently live colonies, total about 8,400 ha. It is believed that the extensive 1930s prairie dog poisoning programs destroyed many of these. The next paper, by Collins and Lichvar, describes vegetation on selected portions of Meeteetse ferret habitat and compares it with vegetation on prairie dog colonies elsewhere in Wyoming that historically provided ferret habitat. The authors conclude that all sites measured were previously disturbed by heavy livestock grazing or other factors and that vegetation is not a useful attribute to define ferret habitat or to locate transplant sites.

Fagerstone and Biggins describe prairie dog populations at Meeteetse serving as prey for ferrets and present a method to census prairie dogs as a means to locate ferret transplant sites. The last paper about ferret habitat by Houston et al. describes a habitat model— a habitat suitability index—useful in locating and comparing transplant sites. It suggests that year-round ferret requirements can be met in prairie dog colonies providing that: (1) prairie dog colonies are large enough, (2) burrows are numerous enough, and (3) adequate numbers of prairie dogs and alternate prey

exist. Five variables are defined and a method to compare prairie dog colony complexes to each other and to Meeteetse is presented.

The third group of papers address ferret behavior, activity patterns, and methods to locate additional ferrets. The Clark et al. paper on descriptive ethology and activity patterns describes an initial ethogram based on observations of 237 ferrets on 441 occasions (208 hrs). Ferrets were active at extremely cold temperatures (-39 C), in rain, snow, and winds to 50 kph. The next paper by Biggins et al. details activity patterns, based on radio tagging, of an adult male and a juvenile female in the fall. Both animals were primarily nocturnal. Peak activity was in early morning hours. The female averaged 1.9 hrs per night above ground (moving 76% and stationary 24%). The last paper in this section by Johnson et al. examines the use of thin-lay chromatography to identify scats to species origin. Twenty known ferret scats were compared with 72 unknown scats. This method was not useful, and analysis with gas-liquid chromatography may prove more definitive.

The two papers in the fourth group discuss the genetic viability of the Meeteetse ferrets and minimum viable population sizes. Kilpatrick et al. found no genetic variation in three proteins examined from saliva samples from 22 ferrets. Comparative data is so limited that it is currently impossible to provide a meaningful interpretation of the lack of genetic variation, but it is similar to results from other carnivore studies and populations that have undergone genetic "bottlenecks." The Groves and Clark paper examines five basic methods of determining the minimum viable population size needed for ferrets: (1) experiments, (2) biogeographic patterns, (3) theoretical models, (4) simulation models, and (5) genetic considerations. The genetic examination proved most useful, resulting in a minimum viable population estimate of about 200 ferrets for maintenance of short-term fitness.

In the fifth section, two papers deal with management and recovery of ferrets. Clark gives management guidelines for the Meeteetse ferrets, describing a series of needed monitoring and protection actions. Comparative data is listed for these actions as well as the public support and organizational ar-

rangements needed for successful overall management and recovery of the species. Richardson et al. present a framework for re covery planning. Three options for increasing ferret numbers are listed and discussed: (1) increase available habitat for the Meeteetse ferrets, (2) find more wild ferrets, and (3) di rectly manipulate ferrets through transloca tion and/or captive rearing. The captive rear ing/translocation option for species recovery is strongly recommended.

The final paper in this monograph by Casey et al. lists 351 annotated references on the ferret. These serve as a solid background for understanding the species and the history of the species' study and conservation efforts.

Collectively these papers, combined with results of the South Dakota studies and com panion papers from the Meeteetse studies published elsewhere, provide much new in formation on the ferret, and, importantly,

they outline management needed to conserve the Meeteetse ferrets and essential actions to recover the species. The vital information needed to conserve and recover the ferret is largely in place—now commitment and ac tion by governmental agencies is called for.

Finally, I personally want to extend my sin cere thanks to all the authors in this monograph, the 40+ reviewers, and the conservation organi zations that financially contributed to its produc tion. Dr. Steve Wood, editor of the *Great Basin Naturalist*, deserves special recognition for his professional management and editing of this vol ume. And, without the full cooperation and friendship of the Meeteetse area ranchers and the conservation community, this volume would have been impossible. My sincere thanks to all.

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PALEOBIOLOGY, BIOGEOGRAPHY, AND SYSTEMATICS OF THE BLACK-FOOTED FERRET, *MUSTELA NIGRIPES* (AUDUBON AND BACHMAN), 1851

Elaine Anderson[1], Steven C. Forrest[2], Tim W. Clark,[2] and Louise Richardson[2]

ABSTRACT.—Extensive literature review and 48 mammal collections containing recent specimens of the endangered black-footed ferret (*Mustela nigripes*) are used to characterize historic distribution of the species. Specimens (n = 120) were measured from eight collections to characterize black-footed ferret morphology and variation. Twenty-one Pleistocene and Holocene faunas in North America show ferrets dating to 100,000 yr B.P. Recent specimens (n = 412) indicate close association with the prairie dog (*Cynomys spp.*) and suggest ferrets may have been less rare than previously thought. At least 103 (25%) of all specimens were taken by federal predator and rodent control agents, and males outnumber females in collections 2.04:1. Average and extreme measurement for external, cranial, and postcranial dimensions are tabulated. Ferrets show a high degree of sexual dimorphism, with discriminant analysis correctly classifying 95% of all specimens to sex. Ferrets also exhibit north-south clinal variation in size, but they do not appear to exhibit variation based on species of *Cynomys* associate. The taxonomic relationship among ferrets and close relatives is described.

The black-footed ferret (*Mustela nigripes*) is a medium-sized musteline that is listed as endangered throughout its former range and currently receives full protection under the U.S. Endangered Species Act of 1973 (16 USC 1531 et. seq.). Endemic to North America, black-footed ferrets formerly occupied an extensive range from the Great Plains of Canada to intermontane regions of the interior Rocky Mountains and southwestern United States. The species is currently known from only one population restricted to an approximately 150 sq km area in northwestern Wyoming (Fig. 1). Decline of the black-footed ferret over the last 50 years is attributed to the often systematic eradication of its principal prey and associate, the prairie dog (*Cynomys spp.*), which is often viewed as an agricultural pest throughout the West. Prairie dogs are semifossorial colonial rodents (Sciuridae) that offer an abundant source of prey and burrows for ferret shelter.

Because black-footed ferrets are primarily nocturnal and spend much of their time underground, they seldom were observed in the wild by naturalists until recent technologies, specifically the high-intensity portable spotlight, made observation possible. Few details of the species biology were known until a small population in Mellette County, South

Fig. 1. Historic range of the black-footed ferret (shaded area) compared with the current known range (dot).

Dakota, was studied from 1964 to 1974. Prior to that time information on distribution and

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specimens of ferrets were collected sporadically by commercial trappers, museum collectors, or federal and state rodent and predator control agents of the U.S. Fish and Wildlife Service (formerly the Biological Survey [BSC] and Bureau of Sport, Fisheries, and Wildlife [BSFW]). Specimens are therefore few and scattered among many collections.

Records of *M. nigripes* specimens and sight reports have been compiled for some states, but no comprehensive record of black-footed ferret distribution based on specimens exists other than Hall (1981). Some authors have included measurements from limited samples, but no systematic analysis based on a large sample has been made. The present study is based on a comprehensive examination and analysis of black-footed ferret remains and literature and describes the paleobiology, distribution, and skeletal morphometry of *M. nigripes*.

Materials and Methods

Sixty-eight mammal collections were contacted and 48 of them reported having *M. nigripes* in their collections. Of these, eight collections were examined and measured. Collection data were supplemented by a thorough literature review. Evidence of ferrets was confirmed either by the presence in museums of specimens (skins, skeletal material) of *M. nigripes* or by observations of ferrets in hand reported in the literature by biologists familiar with the species. Some literature reports, therefore, include live-captured or killed animals that were not collected or preserved as museum specimens. Sight reports or secondary sources, however authentic, were not included.

Collections containing black-footed ferrets are listed below. Asterisks denote collections from which specimens were measured.

AMNH—American Museum of Natural History, New York*
ANSP—Academy of Natural Sciences, Philadelphia
AUG—Augustana College, Sioux Falls, South Dakota
BMS—Buffalo Museum of Science, Buffalo, New York
BNP—Badlands National Park, Interior, South Dakota
BSC—Biological Services Collection, Fort Collins, Colorado*
CDOW—Colorado Division of Wildlife, Denver
CMNH—Carnegie Museum of Natural History, Pittsburg
CSU—Colorado State University, Fort Collins

CU—Cornell University Division of Biological Sciences, Ithaca, New York
DMNH—Denver Museum of Natural History, Denver, Colorado*
FMNH—Field Museum of Natural History, Chicago
HM—Hastings Museum, Hastings, Nebraska
ISU—Iowa State University, Ames
KSU—Kansas State University, Manhattan
KUMNH—University of Kansas, Lawrence*
MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts*
MDFWP—Montana Department of Fish, Wildlife and Parks, Bozeman*
MHM—Minnilusa Pioneer Historical Museum, Rapid City, South Dakota
MSU—Montana State University, Bozeman
NDSHS—North Dakota State Historical Society Museum, Bismarck
NGFP—Nebraska Game, Fish, and Parks, Lincoln
NMC—National Museum of Natural Sciences, Ottawa, Ontario
NSCM—Northwestern State College, Alva, Oklahoma
NYZ—New York Zoological Society, Bronx, New York
NZP—National Zoological Park, Washington, D.C.
OSU—Oklahoma State University, Stillwater
OU—University of Oklahoma, Norman
PAT—Patuxent Wildlife Research Center, Laurel, Maryland
ROM—Royal Ontario Museum, Toronto
SDNHM—San Diego Natural History Museum, San Diego, California
SNMH—Saskatchewan Museum of Natural History, Regina
SYR—State University of New York, Syracuse
SZCM—State Zoological Collection, Munich, German Federal Republic
UCB—University of California, Berkeley
UCM—University of Colorado Museum, Boulder*
UMMZ—University of Michigan Museum of Zoology, Ann Arbor
UMMNH—James Ford Bell Museum of Natural History, University of Minnesota, Minneapolis
UND—University of North Dakota, Grand Forks
UNSM—University of Nebraska State Museum, Lincoln
USD—University of South Dakota, Department of Zoology, Vermillion
USNM—United States National Museum, Washington, D.C.*
UW—University of Wyoming, Laramie.
UWZM—University of Wisconsin Zoological Museum, Madison
WGF—Wyoming Game and Fish Department, Cheyenne
WHO—W. H. Over Museum, University of South Dakota, Vermillion
YPM—Peabody Museum, Yale University, New Haven, Connecticut
ZSP—Zoological Society of Philadelphia

Record localities are listed in Table 6 as they appeared on specimen labels or in the literature, with any comments or clarifying notes included in the text or remarks. Specimen label data were organized by collection date
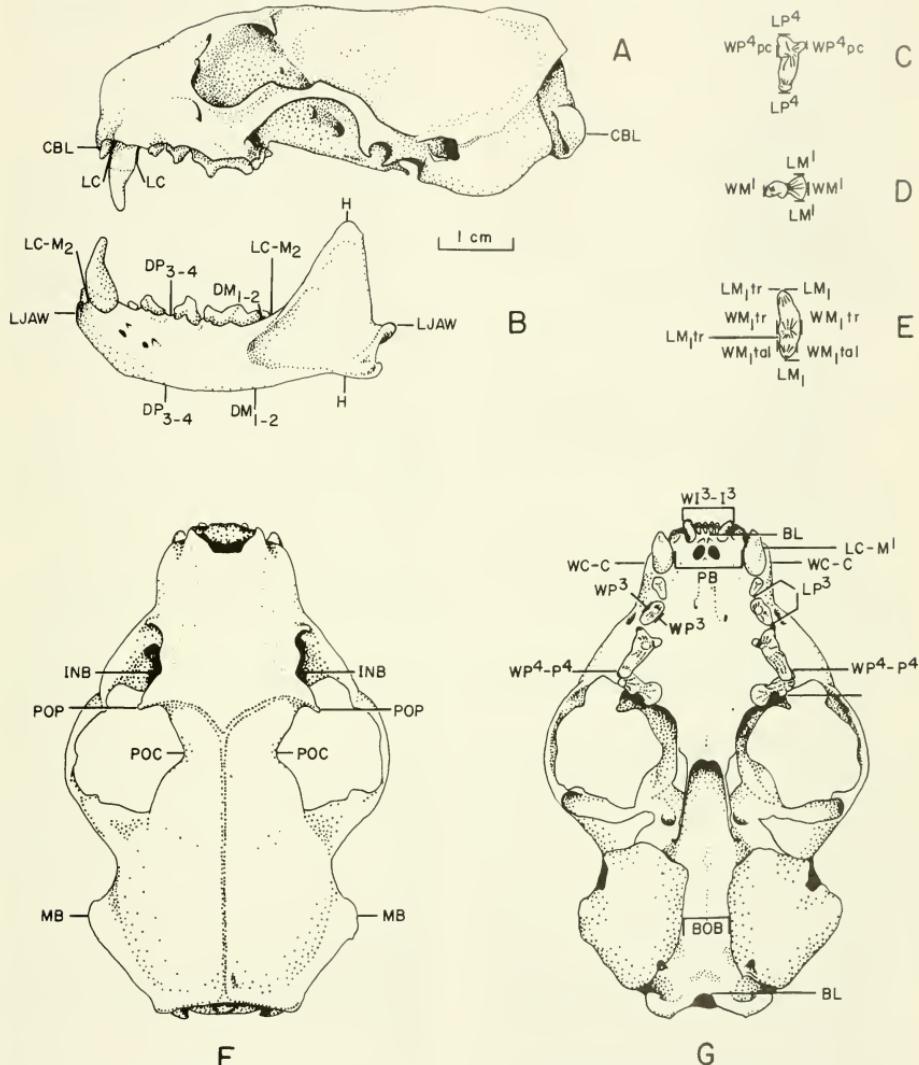
Fig. 2. Skull and mandible of black-footed ferret (Ad. ♂, Baca County, Colorado. DMNH 2248) showing measurements taken. A, Lateral view of skull. B, Lateral view of mandible. C, Occlusal view of P^4. D, Occlusal view of M^1. E, Occlusal view of M_1. F, Dorsal view of skull. G, Ventral view of skull. For symbols see Materials and Methods.

and state or province of collection. Localities (where known) were plotted on maps using dark circles for precise locations and open circles where location was known only to county.

Specimens with one exception were measured by E.A. These included 120 recent

skulls, (72 of known sex), 17 skeletons, and 55 fossil (Pleistocene to Holocene) specimens. In addition, 19 skulls and one skeleton of the Siberian polecat (*M. eversmanni*), a possible Asiatic conspecific of the black-footed ferret, were also measured. Data on external measurements were taken directly from skin tags

and were supplemented by field measurements of live-caught known adult ferrets from the extant population at Meeteetse, Wyoming, from 1982 to 1984.

Measurements of skeletal material were made with vernier calipers to the nearest 1/10 mm. Material was separated by state, species of prairie dog in the locality collected (from the literature), and sex, if known. Figure 2 shows points between which cranial measurements were taken (after Anderson 1970). Cranial measurements taken included:

1. Condylobasal length (CBL). The least distance from a line connecting the posteriormost parts of the occipital condyles to the anteriormost parts of the premaxillae.
2. Basilar length of Hensel (BL). Least distance from a line connecting the anterior border of the foramen magnum to the posterior margin of the first upper incisors.
3. Rostral breadth (WC-C). Width across the rostrum above the canines.
4. Bimolar breadth (WP^4-P^4). Greatest width across the hind cheek teeth measured at the posterior margin of P^4 and the anterior margin of M^1.
5. Interorbital breadth (INB). Least distance across the frontal bones at the fronto-maxillary suture.
6. Postorbital breadth (POP). Greatest width across the postorbital processes.
7. Postorbital constriction breadth (POC). Least width across the frontal bones behind the postorbital processes.
8. Mastoid breadth (MW). Greatest width across the mastoid processes perpendicular to the long axis of the skull.
9. Mandible length (LJAW). Total length from the symphysis at the alveolus of I_1 to the most distant edge of the condyle.
10. Mandible height (H). From the lower border to the tip of the coronoid process.
11, 12. Ramus depth (DP_{3-4}, DM_{1-2}). Depth of the jaw between P_{3-4} and M_{1-2} measured from the level of the alveoli to the lower border.
13. Maxillary tooth row length $(LC-M^1)$. Least distance from the anterior border of the canine at the alveolus to the posterior border of M^1 at the alveolus.
14. Mandibular tooth row length $(LC-M_2)$. Least distance from the anterior border of the canine at the alveolus to the posterior border of M_2 at the alveolus.
15. Incisor breadth (WI^3-I^3). Least width from the buccal side of right I^3 to the buccal side of left I^3.
16. Canine length (LC). The least distance between the anterior and posterior edges of the canine at the level of the alveolus.
17. Canine breadth (WC). Transverse width of the canine at the level of the alveolus.
18, 19. Premolar length (LP^3, LP^4). Least distance from the anterior to the posterior edges of the premolars measured on the buccal side in the plane of the tooth row.
20. Premolar breadth (WP^3). Transverse width of P^3 measured at the center of the cusp.

21. Breadth of protocone of P^4 (WP^4pc). Greatest transverse width from the buccal border of the tooth to the edge of the protocone.
22. Upper molar breadth (WM^1).Greatest transverse width M^1.
23. Upper molar length (LM^1inner). Greatest anterior-posterior length of the inner lobe of M^1.
24. Length of M_1 (LM_1). Greatest anterior-posterior length of M_1 measured on the lingual side.
25. Trignoid length of M_1 (LM_1tr). From the posterior edge of the protoconid to the anterior edge of the tooth.
26, 27. Breadths of M_1 (WM_1 tr, WM_1 tal). Greatest width of the trigonoid measured across the protoconid-metaconid; greatest width of the talonid measured across the hypoconid-entoconid.
28. Palatal breadth at canines (PB C-C). Width of palate between canines.
29. Basioccipital breadth (B OB). Breadth of basioccipital taken at midpoint between bullae.

Postcranial measurements taken included:

Humerus

Total length (TL). Greatest distance from the greater tuberosity to the medial epicondyle.

Proximal breadth (PB). Greatest width across the greater and lesser tuberosities.

Least shaft breadth (LSB). Least diameter of shaft.

Distal breadth (DB). Greatest width across the medial and lateral epicondyles.

Ulna

Total length (TL). Greatest distance from the top of the olecranon to the styloid process.

Breadth olecranon process (B 01 Pr). Maximum width of the olecranon.

Radius

Total length (TL). Greatest distance between the head and the styloid process.

Proximal breadth (PB). Maximum breadth across the head.

Distal breadth (DP). Maximum width of the distal end.

Femur

Total length (TL). Greatest distance from the head to the medial epicondyle.

Proximal breadth (PB). Maximum breadth between the greater trochanter and the head.

Least shaft breadth (LSB). Least diameter of the shaft.

Distal breadth (DB). Greatest distance across the condyles.

Tibia

Total length (TL). Greatest distance between the lateral condyle and the medial malleolus.

Proximal breadth (PB). Maximum breadth between the medial and lateral condyles.

Distal breadth (DB). Maximum width across the distal end.

Fibula

Length (L). Total length between the lateral condyle and the lateral malleolus.

Calcaneum

Length (L). Total length between the calcaneal atuberosity and the cuboid facet.

ASTRAGALUS
Length (L). Greatest perpendicular length of the bone.

BACULUM
Length (L). Greatest length of the bone from the proximal end to the base of the curve.

Specimens were placed in tentative age classes by the following criteria: (1) juvenile: cranial sutures open, deciduous dentition present, but permanent teeth beginning to erupt, epiphyses of long bones not fused; (2) young adult: internasal, nasomaxillary, basisphenoid, and basioccipital sutures fused but not obliterated, permanent dentition fully erupted except for upper canines, teeth unworn or only slightly worn, epiphyses of long bones fused, but sutures still visible; (3) adult: all cranial sutures obliterated, permanent dentition fully erupted, well-developed sagittal crest especially on males, epiphyseal sutures obliterated.

Statistical Methods

Analyses were performed on a Hewlett Packard 3000 computer using the Statistical Package for the Social Sciences (SPSS), including Discriminant Analysis and One-way Analysis of Variance (ANOVA). Linear discriminant analysis was performed between sexes using standardized measurements and confined to specimens of known sex. Juveniles were ommitted from the analysis to avoid allometric variation. Ranges, means, and standard deviations were calculated for both sexes of *M. nigripes*. Scattergrams and frequency diagrams were used to describe relationships between fossil and recent material and interspecies comparisons. A second linear discriminant analysis was performed on standardized cranial measurements of male and female ferrets to identify groups based on geographic variation and subgenera of prairie dog associate. One-way analysis of variance (ANOVA) was used to explore further variation of individual variables with regard to geographic clinal variation.

DESCRIPTION

Mustela nigripes (Audubon & Bachman)

Putorius nigripes Audubon & Bachman 1851: 297. Type locality Ft. Laramie, Goshen Co., Wyoming.
Mustela nigripes Miller 1912: 102. First use of binomial. No subspecies are recognized.
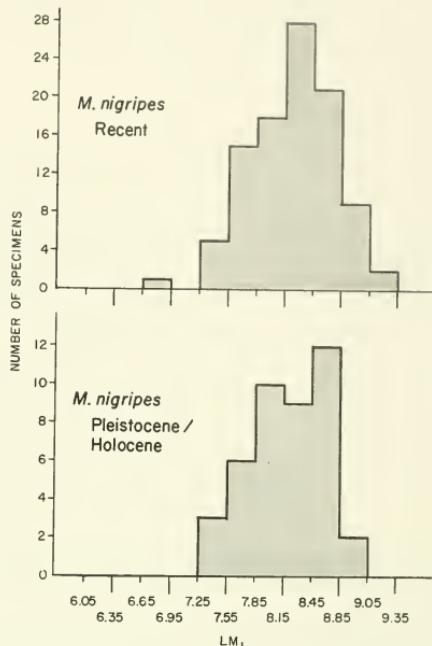
Fig. 3. Frequency histogram of length of M_1 for Recent, Pleistocene, and Holocene specimens.

DIAGNOSIS.—*Mustela nigripes* is a mink-sized mustelid weighing 645–1125 g. Upper parts yellowish buff, occasionally whitish, especially on the face and venter; feet black; black mask across the eyes, particularly well defined in young animals; tail black tipped. Skull is relatively short and broad; mastoid process is notably angular (Hillman and Clark 1980). Closely resembles *M. eversmanni*, the steppe ferret of Eurasia. Differs from *M. putorius*, the European ferret, and *M. vison*, the American mink, in being light colored with black markings; the latter two species are uniformly dark colored, and *M. p. furo*, the domestic ferret, is uniformly light colored, often albinistic.

Morphometry

Data on external measurements for Recent material were taken directly from skin tags and are supplemented with field measurements of live-caught juvenile and adult ferrets from Meeteetse from 1982 to 1984. Average (± S.D.) and extreme external measurements
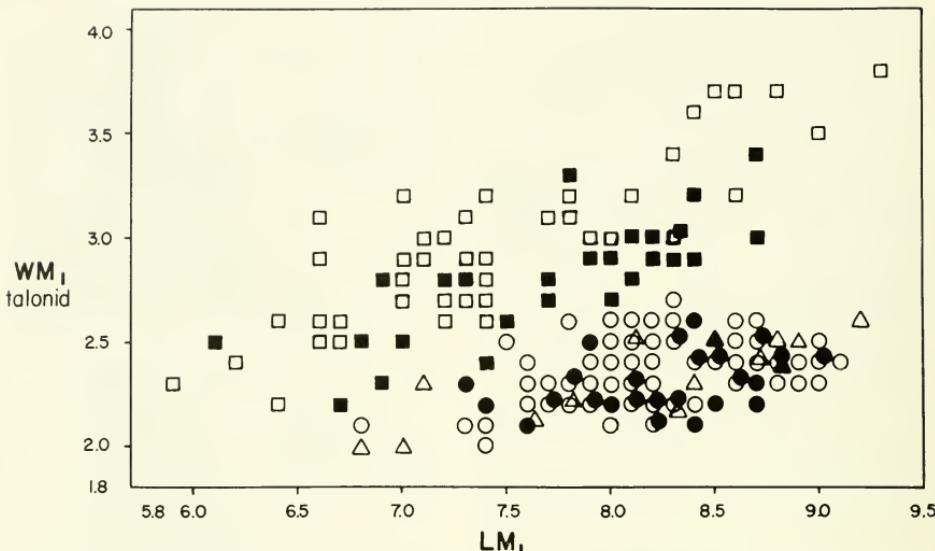
Fig. 4. Relationship between the width of M_1 talonid and the length of M_1 for *Mustela nigripes* (circles), *M. eversmanni* (triangles), and *M. vison* (squares) for Recent (open symbols) and Pleistocene (solid symbols) material.

in mm for adults are: Adult males (skin tags): total length (n=20) 533.8 ± 28.98, 490–600; tail (n=19) 123.0 ± 10.47, 107–140; hind foot (n=19) 61.4 ± 5.46, 51–70. Adult males (Meeteetse, field measured): total length (n=12) 566.8 ± 29.00, 517–615; tail (n=12) 137.0 ± 8.95, 119–148; hind foot (n=12) 64.1 ± 3.17, 59–65; ear (n=12) 28.2 ± 2.45, 25–34; weight (n=13) 1034.3 ± 60.18, 915–1125. Adult females (skin tags): total length (n=7) 501.1 ± 13.79, 479–518; tail (n=7) 119.0 ± 8.46, 109–132; hind foot (n=7) 59.8 ± 2.67, 56–63. Adult females (Meeteetse, field measured): total length (n=21) 532.0 ± 17.00, 496–565; tail (n=22) 132.2 ± 7.62, 120–141; hind foot (n=21) 57.2 ± 2.90, 51–62; ear (n=21) 25.6 ± 1.55, 23–28; weight (n=31) 703.5 ± 128.36, 645–850.

Young of the year measured in August and September are classified as juveniles and all others as adults. Juvenile males caught in October averaged total lengths of 578.0 ± 16.11 mm and weighed 943.5 ± 134.27 g. Juvenile females were 536.4 ± 22.20 mm in total length and weighed 700.6 ± 36.60 g. These measurements fall within adult ranges, indicating juveniles are externally as large as adults by about the time they reach independence in October. Differences between mu-

seum and field-measured groups are probably related to measuring errors under field conditions with live animals and do not represent real size differences between specimens. Since field measurements were taken consistently, their relative values are similar.

Comparisons of the Pleistocene material with Recent specimens showed no differences in size or morphology. Of the nine mandibular characters for which data were available, none significantly differed from recent material in frequency plots (Fig. 3) or in scattergrams (Figs. 4, 5, 6). Data on fossil remains was most consistently available for mandibular and dental characters. Only 29 values for 16 cranial characters from 11 specimens were available. Table 1 shows cranial measurements for Pleistocene material assigned to sex based on the discriminant analysis for Recent material.

The skull of *M. nigripes* is relatively short and broad with large postorbital processes and widely spreading zygomatic arches. It has a short convex rostrum, a slight facial angle, obliquely flattened auditory bullae, and a narrow basioccipital region. In adult males the sagittal and lambdoidal crests are well developed and the mastoid processes are angular and projecting. The postorbital constriction is pronounced, unlike the condition in *M. puto-*
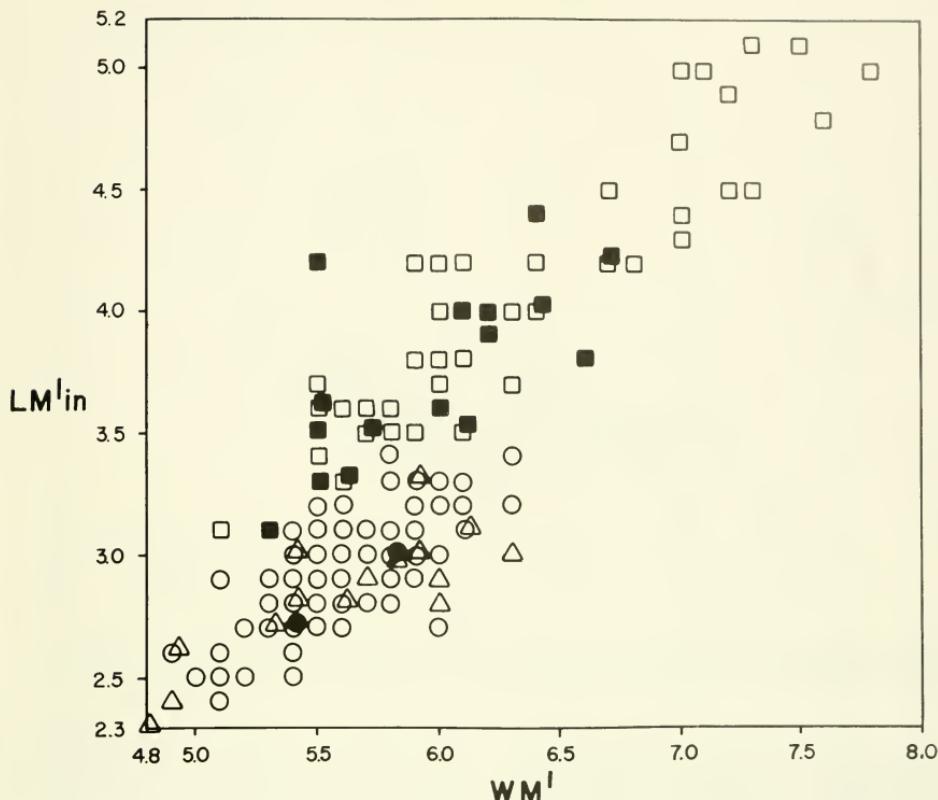
Fig. 5. Relationship between the length of M¹inner lobe and the width of M¹ for *Mustela nigripes* (circles), *M. eversmanni* (triangles), and *M. vison* (squares) for Recent (open symbols) and Pleistocene (solid symbols) material.

TABLE 1. Mandibular and dental dimensions for Pleistocene specimens of *M. nigripes*. For symbols used in Column 1 see Cranial Measurements under Materials and Methods.

|	Sex	Number	Minimum	Mean	Maximum	S. D.
LJAW	M	4	41.9	42.2	42.6	0.29
	F	9	34.7	38.0	40.3	1.96
H	M	6	19.5	20.5	21.8	0.86
	F	7	16.1	18.5	19.7	1.25
DP_{3-4}	M	18	8.4	9.0	10.0	0.43
	F	14	6.5	7.5	8.4	0.54
DM_{1-2}	M	18	7.8	8.7	9.9	0.51
	F	15	6.8	7.7	9.1	0.54
$LC-M_2$	M	8	23.9	24.9	25.3	0.47
	F	9	20.4	22.1	23.5	0.96
LM_1	M	19	7.8	8.5	9.0	0.29
	F	18	7.3	7.9	8.4	0.34
LM_1tr	M	19	5.6	6.1	6.3	0.21
	F	17	5.2	5.6	6.2	0.25
WM_1tr	M	16	2.8	3.2	3.6	0.22
	F	15	2.5	2.8	3.1	0.23
WM_1tal	M	19	2.2	2.3	2.6	0.17
	F	18	2.0	2.2	2.3	0.09
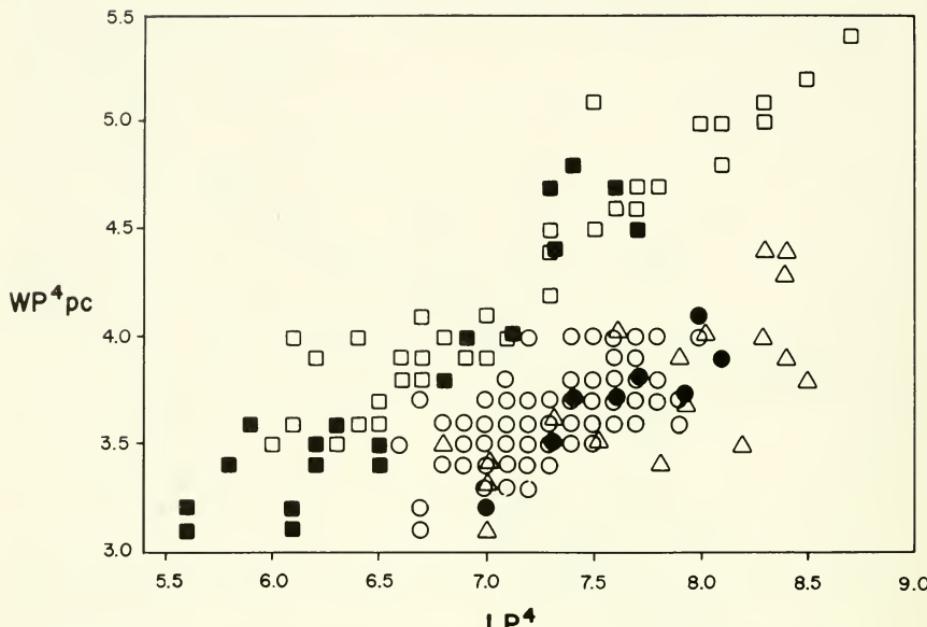
Fig. 6. Relationship between the width of P^4 protocone and the length of P^4 for *Mustela nigripes* (circles), *M. eversmanni* (triangles), and *M. vison* (squares) for Recent (open symbols) and Pleistocene (solid symbols) material.
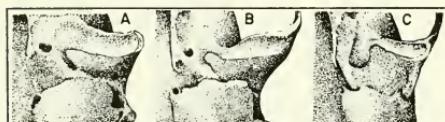
Fig. 7. Portion of basicranium of *Mustela nigripes* showing the well-defined tube enclosing the foramen ovale and extending posterolaterally to the anterior margin of the auditory bulla. Compared with *M. vison*. A, *M. nigripes* from Little Box Elder Cave (UCM 21952). B, *M. nigripes* Recent (UCM-S 263). C, *M. vison* Recent (UCM 7449) (from Anderson 1968).

rius. The broad palate extends beyond the last molar. Anderson (1968:32) described the characteristic basicranium as follows:

Black-footed ferret skulls have a well-defined tube enclosing the foramen ovale and extending postero-laterally to the anterior margin of the auditory bulla. Anteriorly the tube is emarginate with the post-glenoid process and opens just anterior to the pterygoid process. The foramen ovale pierces the alisphenoid; immediately anterior to it is the foramen rotundum.

The tube is absent in mink (Fig. 7) and is useful in distinguishing the two species.

Sagittal crest formation has been used to age ferrets in the field with some success (Thorne et al. 1985). Animals of both sexes may be classed as either juveniles or adults on the basis of the definition and sharpness of the crest, which is generally not prominent in animals less than 6 months in age but fairly defined in one-year-old animals. It initially increases in prominence with age and then flattens out.

The mandible is relatively short and thick, and the inferior margin at the angle is broad and flattened. The masseteric fossa extends anteriorly to the middle of the talonid of M_1. The mental foramina, usually four in number, are located below P_{2-3} and P_{3-4}. Average and extreme cranial measurements are shown in Table 2.

The dental formula of *M. nigripes* and the other ferrets and mink is i 3/3, c 1/1, p 3/3, m 1/2, for a total of 34 teeth that are set close together but do not overlap. The incisors are small and the upper ones are set in a straight row separated from the canines by a short diastema; the lower incisors are crowded with

Table 2. Cranial and dental dimensions for *M. nigripes* (Recent).

	Sex	N	Minimum	Mean	Maximum	S.D.
CBL	M	45	64.1	68.0	70.8	1.62
	F	23	58.1	63.3	67.5	2.47
BL	M	44	58.6	62.4	65.5	1.56
	F	24	53.0	58.0	61.7	2.25
WC-C	M	47	16.0	17.7	19.0	0.65
	F	24	14.2	16.0	17.2	0.77
WP^4-P^4	M	48	22.3	24.3	25.9	0.77
	F	24	20.4	22.6	23.6	0.98
INB	M	49	16.2	17.6	19.5	0.76
	F	24	14.8	15.9	17.4	0.65
POP	M	48	19.8	21.7	23.8	1.24
	F	24	18.4	19.6	22.5	1.04
POC	M	46	9.8	12.7	15.3	1.01
	F	24	10.0	12.1	14.5	1.18
MW	M	46	30.4	36.5	40.1	1.58
	F	23	28.8	33.7	36.3	1.65
$LC-M^1$	M	46	19.1	20.3	21.9	0.62
	F	24	17.5	19.0	20.8	0.79
LC	M	47	3.7	4.3	4.8	0.20
	F	24	3.2	3.8	4.2	0.24
WC	M	47	3.0	3.3	3.6	0.17
	F	24	2.7	2.9	3.2	0.14
LP^4	M	49	7.0	7.5	8.0	0.24
	F	24	6.7	7.1	7.5	0.23
WP^4_{pc}	M	49	3.3	3.7	4.0	0.18
	F	24	3.1	3.5	3.8	0.17
WM^1	M	49	5.2	5.7	6.3	0.26
	F	24	4.9	5.4	5.8	0.25
LM^1	M	49	2.7	3.0	3.4	0.18
	F	23	2.4	2.8	3.1	0.21
LJAW	M	47	40.4	43.1	45.6	1.34
	F	24	35.2	39.5	43.1	1.90
H	M	45	18.7	21.0	22.2	0.75
	F	24	17.0	19.2	21.4	1.12
DP_{3-4}	M	46	7.8	8.7	9.5	0.39
	F	24	7.1	7.9	8.8	0.44
DM_{1-2}	M	47	7.7	9.0	10.0	0.48
	F	24	7.1	8.1	9.1	0.52
$LC-M_2$	M	46	23.2	24.6	26.1	0.66
	F	23	20.5	22.7	24.4	0.93
LM_1	M	48	7.7	8.4	9.1	0.37
	F	24	6.8	7.9	8.4	0.40
LM_1tr	M	47	5.6	5.9	6.4	0.20
	F	23	5.1	5.5	6.0	0.22
WM_1tr	M	48	2.7	3.1	3.5	0.16
	F	24	2.6	2.9	3.2	0.17
WM_1tal	M	47	2.2	2.4	2.6	0.11
	F	24	2.0	2.2	2.8	0.17
WI^3-I^3	M	38	6.0	6.5	7.2	0.29
	F	23	5.1	6.0	6.6	0.39
WBC	M	35	8.3	9.4	10.3	0.46
	F	30	7.7	8.6	9.4	0.45
BOB	M	37	6.1	7.2	9.1	0.67
	F	32	5.9	6.7	7.7	0.48
LP^3	M	40	3.6	3.9	4.2	0.16
	F	35	3.2	3.7	4.0	0.20
WP^3	M	40	2.0	2.2	2.5	0.13
	F	35	1.7	2.1	2.3	0.14

I_2 set back of I_1 and I_3. The canines are relatively large and slightly curved. The anterior premolars ($P^{2\text{-}3}$, $P_{2\text{-}4}$) are double-rooted, relatively short and broad, and single-cusped. The upper carnassial (P^4) is trenchant with a relatively small protocone; the width of the tooth across the protocone is less than that of mink (Fig. 22). P^4 is longer than the width of M^1. The upper molar (M^1) has the characteristic hourglass shape of the Mustelinae, but the inner lobe is not as expanded as that of mink (Fig. 5). There is no trace of a metaconid on the lower carnassial (M_1) and the trigonid is longer than the talonid; ferrets have a nar- rower talonid than do mink (Fig. 4). M_2 is relatively small, and circular in shape. Fig- ures 4, 5, and 6 show that measurements of *M. nigripes* fall within the range of *M. evers- manni*.

No supernumerary teeth were observed. In a few mandibles P_2 (2 specimens) or M_2 (4 specimens) was absent and the alveolus closed; whether the tooth had been lost and the alveolus closed during the life of the ani- mal or whether the tooth had never erupted could not be determined. Only one specimen (USNM 21976) had an abcessed tooth (P^4). Ruprecht (1978) noted deviations in the num- ber of teeth in *M. putorius* in Poland and Holland. With advanced age the tooth cusps become worn smooth and the canines, per- haps broken earlier in life, are stubby and rounded. No studies are available on the se- quence of eruption of the teeth of *M. nigripes*, nor have there been any studies on age deter- mination by counting the annuli in tooth ce- mentum or using radiographs to determine the size of the pulp cavity of the canine. Aver- age and extreme dental measurements are shown in Table 2.

The appendicular skeleton of the black- footed ferret is unspecialized and shows no extreme modifications as are seen in badgers and otters. The shafts of the limb bones are relatively straight, the proximal and distal ends are not greatly expanded, and processes are not overly developed. The calcaneum has a well-developed trochlear process, and the posterior articular surface is rounded and smooth (Stains 1966). Only a few limb bones of *M. nigripes* have been recognized in Pleis- tocene faunas (Little Box Elder, Jaguar, and Isleta caves); their measurements fall within those of Recent specimens. Table 3 gives postcranial dimensions of Recent *M. nigripes*. Compared with mink, the limb bones of fer- rets tend to be more rugose and show less curvature, but it is difficult to separate the two species when only limb bones are available.

The baculum of *M. nigripes* is similar to that of mink in having the distal end hooked sharply backward. In young animals the prox- imal end is a simple, laterally flattened base that with age develops a collar and becomes quite rugose. The ventral groove extends more than half the length of the shaft (Burt 1960). Eight bacula were examined and mea- sured; the Pleistocene specimen from Isleta Cave (Fig. 8) was identical in size and mor- phology to the Recent material.

Life history

The black-footed ferret is a mostly noctur- nal, solitary carnivore. The range of the black- footed ferret is sympatric with that of the prairie dog (*Cynomys*) throughout North America, and breeding populations of ferrets have only been found in association with prairie dog colonies (Linder et al. 1972, For- rest et al., *Black-footed ferret habitat*, 1985). Ferrets live in the burrows made by prairie dogs and exploit prairie dogs as their major food source (Sheets et al. 1972). Ferrets also eat lagomorphs, mice (cricetids), voles (mi- crotines), ground squirrels and pocket go- phers (geomyids), birds, and insects (Hender- son et al. 1969; Clark et al. 1985).

Breeding occurs in March-April. Coitus lasts from 1.5 to 3 hours, and gestation is approximately 42–45 days (Carpenter and Hillman 1978). Litter sizes range 1–5 young and average 3.3–3.4/litter (Linder et al. 1972, Forrest et al., *Life history characteristics*, 1985). Juveniles first appear aboveground in late June. The sex ratio at this time is equal (Forrest et al., *Life history characteristics*, 1985).

Primary mortality sources for black-footed ferrets are unknown. Potential predators of ferrets include: badgers (*Taxidea taxus*), coy- otes (*Canis latrans*), bobcats (*Lynx rufus*), golden eagles (*Aquila chrysaetos*), great- horned owls (*Bubo virginianus*), and hawks (Henderson et al. 1969; Forrest et al. *Litter survey*, 1985). Forrest et al. (*Life history characteristics*, 1985) identified four major

TABLE 3. Postcranial dimensions, Recent *M. nigripes*. For symbols used in column 1 see Materials and Methods.

Bone	Sex	N	Minimum	Mean	Maximum	S.D.
HUMERUS						
TL	M	11	46.0	49.5	52.0	1.79
	F	2	45.5	46.2	47.0	—
PB	M	11	9.9	10.7	11.7	0.59
	F	2	10.0	10.2	10.4	—
LSB	M	10	3.5	3.8	4.1	0.20
	F	1	—	3.3	—	—
DB	M	11	12.3	13.0	13.8	0.57
	F	2	11.4	11.8	12.2	—
ULNA						
TL	M	10	44.4	46.6	48.6	1.36
	F	2	42.9	43.8	44.7	—
B 01 Pr.	M	11	5.5	5.7	6.2	0.30
	F	2	5.3	5.6	5.8	—
RADIUS						
TL	M	10	33.5	36.0	37.2	1.16
	F	2	32.9	33.9	34.9	—
PB	M	11	4.8	5.6	6.0	0.33
	F	2	5.1	5.4	5.6	—
DB	M	10	6.2	6.9	7.4	0.39
	F	2	6.2	6.4	6.6	—
FEMUR						
TL	M	11	47.1	51.3	53.7	2.05
	F	2	46.7	47.9	49.1	—
PB	M	11	11.7	12.7	13.5	0.59
	F	2	11.0	11.4	11.7	—
LSB	M	10	4.1	4.4	4.8	0.28
	F	2	3.9	4.2	4.4	—
DB	M	11	9.5	10.8	11.6	0.55
	F	2	9.4	9.9	10.4	—
TIBIA						
TL	M	11	48.3	51.5	54.4	1.75
	F	3	47.1	48.4	49.8	1.36
PB	M	11	9.8	10.7	11.4	0.51
	F	3	9.2	10.1	10.6	0.75
DB	M	11	7.1	7.8	8.1	0.32
	F	3	7.1	7.3	7.5	0.21
T L. FIBULA	M	10	44.9	47.2	48.7	1.11
	F	1	—	43.1	—	—
T. L. CALCANEUM	M	10	13.0	13.6	14.8	0.49
	F	1	—	12.3	—	—
T. L. ASTRAGALUS	M	8	8.5	8.9	9.3	0.32
	F	1	—	7.6	—	—
T. L. BACULUM	M	8	31.2	36.9	40.0	2.64
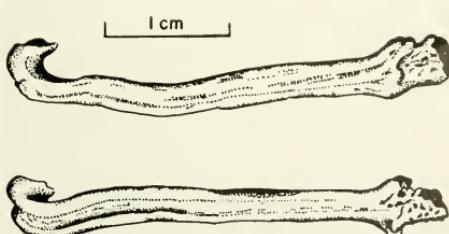
Fig. 8. Baculum of *M. nigripes* (Isleta Cave A 2967; total length 35.5 mm).

sources of mortality (predation, disease, man-caused, and resource related) and suggested from comparative studies of other *Mustela* species that average life span of ferrets in the wild is probably less than one year; there is preliminary evidence of high juvenile mortality at Meeteetse.

Forrest et al. (*Black-footed ferret habitat*, 1985) estimate ferret distribution at Meeteetse at about 40–60 ha/ferret and noted that large prairie dog colonies (greater than 40 ha) support most female ferrets with litters. Large

TABLE 4. Black-footed ferret remains from Pleistocene, Early Holocene, and archeological faunas and steppe ferret remains from the Pleistocene of Alaska.

Fauna	Location	Age	Ferrets Minimum number	Number of specimens
Cudahy	Kansas, Meade Co.	Late Irvingtonian	1	1
Adams Co.	Nebraska, Adams & Clay Cos.	? Late Illinoian	1	1
Medicine Hat	Alberta, Canada	Sangamonian	1	1
Moore Pit	Texas, Dallas & Denton Cos.	> 30,000 yrs. B.P.	1	1
"Citellus" beds	Nebraska, Lincoln Co.	28,000–30,000 yrs. B.P.	1	3
Cottonwood Canyon	Nebraska, Lincoln Co.	28,000–30,000 yrs. B.P.	1	1
Smith Falls	Nebraska, Cherry Co.	Wisconsin	1	1
Harlan Co. Dam Site	Nebraska, Harlan Co.	Wisconsin	1	2
January Cave	Alberta, Canada	23,100–33,500 yrs. B.P.	2	7
Little Box Elder Cave	Wyoming, Converse Co.	9,000- > 30,000 yrs. B.P.	15	40
Chimney Rock Animal Trap	Colorado, Larimer Co.	11,980 ± 180	1	1
Burnet Cave	New Mexico, Eddy Co.	11,170 ± 360	1	1
Jaguar Cave	Idaho, Lemhi Co.	10,370 ± 350	2	12
Little Canyon Creek Cave	Wyoming, Washakie Co.	10,170 ± 250	1	1
Orr Cave	Montana, Beaverhead Co.	Late Pleistocene	1	1
Old Crow River, Location 65	Yukon Territory, Canada	Late Pleistocene	1	1
Isleta Cave	New Mexico, Bernalillo Co.	Late Pleistocene/ early Holocene	2	6
Red Willow	Nebraska, Red Willow Co.	Late Pleistocene/ early Holocene	1	1
Moonshiner Cave	Idaho, Bingham Co.	Early Holocene	1	2
Atlatl Cave	New Mexico, San Juan Co.	2,000–3,000 yrs. B. P.	1	1
Ashislepha Shelter	New Mexico, San Juan Co.	Archaic	1	1
Upper Plum Creek	Colorado, Las Animas Co.	570 ± 50–1,050 ± 80 AD	2	4
Mustela eversmanni beringiae				
Fairbanks	Alaska, near Fairbanks	Late Pleistocene	2	3

clusters of prairie dog colonies appear necessary to support populations. The lack of such colonies in highly developed prairie lands is suspected as the principle cause of ferret en dangerment, although possible catastrophic losses of prey base due to sylvatic plague in prairie dogs has also been discussed (Hubbard and Schmitt 1984).

DISTRIBUTION

Pleistocene and Paleo-Indian Distribution

Ferrets have been identified from 21 Pleis tocene and Holocene faunas in North America (Table 4). Two ferret species, *Mustela evers- manni* from Fairbanks, Alaska (Anderson 1977) and *M. nigripes* are recognized. Six oc currences of *M. nigripes* are outside the his toric range (Fig. 9) of this species.

The earliest occurrence of *M. nigripes* is uncertain, but the species has probably been present in North America since the Sangamo-

nian about 100,000 years ago. The specimen from the Cudahy fauna, an isolated left M^1 (University of Michigan Museum of Verte brate Paleontology #38341) was originally identified as *Mustela* cf *vison* by Getz (1960), who noted slight differences between it and the comparative material. Later Hibbard (1970) referred the specimen without com ment to *M. nigripes* and Corner (1977) fol lowed this designation. Examination of the tooth showed the presence of an incipient metaconid, a characteristic of mink but not ferret. Measurements of the tooth of the two species are not diagnostic. The age of the Cud ahy fauna is Irvingtonian (Type 0, Pearlette Ash, 600,000 yrs B.P.), and the habitat was marshy with permanent, slow-moving streams; numerous species of aquatic and semiaquatic animals have been identified. Mink have been identified from other Irvingtonian faunas, fer rets have not. Thus, the identity of this tooth remains questionable. We follow Getz's (1960)

Prey species	Remarks	References
No *Cynomys*, many spp. rodents	? Id. Originally identified as *M. vison*; see text	Getz 1960, Hibbard 1970
		L. Martin, pers. comm.
Cynomys leucurus	Grassland, warmer than today	Stalker et al. 1982
No *Cynomys*, many spp. rodents	Originally identified as *M. vison*	Slaughter 1966
No *Cynomys*, many spp. rodents	Age originally thought to be Sangamonian	Dreeszen 1970 Corner,
		pers. comm.
No *Cynomys*, rodents abundant	May be "Citellus" zone in part; open prairie	R. G. Corner, pers. comm.
Cynomys sp.	Steppe	Voorhies and Corner, in press
No *Cynomys*, many spp. rodents	Articulated skull and mandible; open prairie	R. G. Corner, pers. comm.
Cynomys leucurus		J. Burns, pers. comm.
Cynomys leucurus		Anderson 1968, 1974
Cynomys sp.		Hager 1972
Cynomys ludovicianus	? Id. Juvenile; deciduous dentition	Schultz and Howard 1935
No *Cynomys*, many spp. rodents	Outside historic range	Kurtén and Anderson 1972
No *Cynomys*, many spp. rodents		D. Walker, pers. comm.
No *Cynomys*	Outside historic range	Guilday and Adam 1967
No *Cynomys*	Outside historic range, cool grassland	C. R. Harington, pers. comm.
Cynomys gunnisoni		Harris and Findley 1964
Cynomys ludovicianus		Corner 1977, pers. comm.
No *Cynomys*, many spp. rodents	Carnivore trap; outside historic range	White et al. 1984
	Specimen burned	J. Hubbard, pers. comm.
Cynomys gunnisoni		W. Gillespie, ms. and
		pers. comm.
104 *Cynomys ludovicianus*	1 specimen burned, 2 found in bone cache	Anderson, ms.
No *Cynomys*, many spp. rodents, lagomorphs	Cool grassland. Only record of *M. e.* in North America	Anderson 1977

designation of *M.* cf *vison*. The next earliest record of ferret may be late Illinoian/early Sangamonian (Adams/Clay counties, Nebraska, exact age uncertain; the specimens from the "Citellus" beds were originally thought to be the same age but are now regarded as late Wisconsinan in age) or Sangamonian (Medicine Hat), about 100,000 yrs B.P. By the late Wisconsin/early Holocene (15,000–8,000 B.P.), ferrets ranged across the Great Plains west to Montana (Orr Cave) and Idaho (Jaguar, Moonshiner caves) and even as far north as Yukon Territory (Old Crow). At most sites only a few bones representing one individual have been found, but at Little Box-Elder Cave at least 40 specimens and 15 individuals (based on left mandibles) have been identified. The site, in the foothills of the Laramie Mountains, contains a large number of prey animals including *Cynomys* cf *leucurus* (n=77+). Prairie dogs have been found in

10 of the faunas containing ferrets. The other sites did not contain prairie dogs, but various rodent and lagomorph species were abundant. At two archeological sites, Atlatl Cave and Upper Plum Creek Rockshelter, burned ferret bones were found, indicating their possible use by Paleoindians.

During the late Pleistocene the steppe ferret, *M. eversmanni*, ranged east to Beringia, the vast unglaciated land mass that extended from northeastern Siberia to western Alaska. Its remains have been found in deposits near Fairbanks, Alaska (Anderson 1973, 1977). The specimens, a partial skull and two mandibles, are characterized by large size, broad facial region, massive postorbital processes, pronounced postorbital constriction, crowded tooth row, and enlarged canines. Measurements exceeded those of *M. eversmanni michnoi*, the largest extant subspecies. Anderson (1977) described the material as a new subspe-

Fig. 9. Distribution of black-footed ferrets in Pleis tocene, early Holocene, and archeological faunas com pared with its historic range (1851–1920).

cies, *M. e. beringiae*, and noted that it is the first and only record of the steppe ferret in North America.

In the Old World ferrets are recognized in middle Pleistocene faunas in central Europe, but whether the fragmentary remains are of *M. putorius* or *M. eversmanni* is unknown. By the late Pleistocene remains of *M. putorius* are common in Eurasian cave faunas. *Mustela eversmanni* has been reported from late Pleis tocene/Holocene faunas in Siberia, Crimea, and the Russian plains and from Holocene faunas in the Caucausus and central Asia (Vereshchagin and Baryshnikov 1984).

Early Historic Record

The first possible report of *M. nigripes* by a European may be attributed to Don Juan de Oñate, a Spanish explorer of what is now the southwestern U.S. in 1599.

It is a land (New Mexico Territory) abounding in flesh of buffalo, goats with hideous horns, and turkeys; and in

Mohoce there is game of all kinds. There are many wild and ferocious beasts, lions, bears, wolves, tigers, penicas, *ferrets*, porcupines, and other animals, whose hides they tan and use. (Bolton 1916: 217; italics ours).

Both domestic (*M. putorius furo*) and wild European polecats (*M. p. putorius*) were common in Europe at that time, so Oñate could have correctly identified the North American counterpart. It is possible he could have confused ferrets with other *Mustela* that have no comparable Old World counterparts, particularly the "bridled" weasels (color morphs of *M. frenata*: *M. f. arizonensis* and *M. f. neomexicana*) of the southwest. Since Mohoce (also "Moqui," the center of the Hopi nation, in the vicinity of present-day Walupi, Arizona) is within known black-footed ferret range, it appears equally likely that what Oñate described was in fact a black-footed ferret.

Several ethnographically known tribes were familiar with and used black-footed ferret skins in ceremonial dressings (Henderson et al. 1969, Clark 1975). Tribes with knowledge of black-footed ferrets ranged from the Navaho of northern Arizona and New Mexico to the Hidatsas of the upper Missouri River Basin (Table 5).

Ferrets were also reported in the records of the American Fur Company from 1835 to 1839 (Johnson 1969). Pratte, Chouteau, and Company of St. Louis listed pelts of 86 black-footed ferrets taken during this period. Trap pers were familiar with mustelids ("weasels" are listed separately from ferrets in this tally) and probably accurately identified the species long before it was scientifically named and described by Audubon and Bachman (1851). It was Alexander Culbertson, a trapper, who first brought the species to the attention of Audubon. Known as the "French Fur Com pany," Pratte, Chouteau, and Company be came the Western Department of the Ameri can Fur Company, concentrating most of their effort in the upper Missouri River basin. They operated for some time out of Ft. Kiowa near the junction of the White and Missouri rivers in present-day South Dakota (Morgan 1953). Their license was for "Sioux Country," which encompassed parts of present-day South Dakota, Montana, and Wyoming.

TABLE 5. Black-footed ferret specimens associated with ethnographically known Indian tribes.

Ethnographic tribe	Tribal name for BFFs	Specimen type	No. of specimens	Disposition	Citations
Blackfoot	?	chief's headdress	1	?	Homolka 1964
Cheyenne	?	chief's headdress	?	?	Henderson et al. 1969
Crow	?	medicine pouch	4	Chief Plenty Coups Museum, Pryor, Montana	
		medicine pouch	2	Plains Indian Museum, Cody, Wyoming	
		skin	2	Plains Indian Museum, Cody, Wyoming	
		skin	1	Colter Bay Indian Museum, Grand Teton National Park, Wyoming	
Hidatsas	"Tahu akukahak napish"				Bailey 1926
Mandan	"Nazi"				Bailey 1926
Navajo	"dlo'ii liz-hinii"	"pelts"	"several"		Fortenbery 1971, Halloran 1964
Pawnee	"ground dogs" in a mythical story; speaks of itself as "staying hid all the time"				Grinnell 1895, 1896
Sioux	"pispiza etopta sapa," "black-faced prairie dog"	skins, sacred tribal objects	2	St. Francis, South Dakota	Henderson et al. 1969

Recent Distribution

John James Audubon and John Bachman (1851) named and described *Mustela nigripes* from a specimen collected near Fort Laramie, in what is now Goshen County, Wyoming. This specimen was either lost or destroyed, and subsequently naturalists questioned whether the species actually existed (Gray 1865). Elliot Coues (1874:1), curator of the Smithsonian mammal collection, published a plea in the *American Sportsman* for additional specimens likely to be found "out on the plains in the prairie dog towns." Coues was rewarded with several specimens and ac counts of black-footed ferrets, which he sub sequently described (Coues 1877).

Table 6 gives a comprehensive listing of each known ferret specimen by state. Black footed ferrets have been found with three spe cies of *Cynomys*: *C. ludovicianus* (black tailed prairie dog), *C. leucurus* (white-tailed prairie dog), and *C. gunnisoni* (Gunnison's prairie dog). Since *M. nigripes* distribution and abundance is highly dependent on prairie dog distribution and abundance, we include discussion of the past and present range of *Cynomys*. Because genetic "bottlenecks" occur when species numbers are low and may be criti cal for species survival (Soule 1980), an estimate of habitat available to ferrets based on prairie dog distribution at their lowest point is also given where known.

Arizona

Four specimens of *M. nigripes* are known for Arizona (Table 6, Fig. 10). The last specimen was collected in Coconino County in 1931. Two of these specimens from the U.S. National Mu seum were described by Young and Halloran (1952).

Historically two species of prairie dogs, *C. ludovicianus* and *C. gunnisoni*, inhabited Arizona. The ferrets were all collected within the range of *C. gunnisoni*. *Cynomys ludovicianus* was proba bly extirpated in Arizona as early as 1932 (Alex ander 1932) and no longer exists in the state (Cockrum 1960). Current distribution of *C. gun nisoni* is also greatly reduced, although relict populations of sufficient size to support black footed ferrets may persist in the northeastern cor ner of the state. The historic, as well as present area occupied by prairie dogs is unknown.

TABLE 6. Recent black-footed ferret specimen accounts by state, 1851–1984.

Year	Date	Disposition	County	Site	Sex	Skel-eton	Crania	Skin
ARIZONA								
1917	Jan 19	USNM 228233	Apache	Springerville, 27 km NE	M		X	X
1929	Jan	USNM 248973	Coconino	Williams, N Red Lake	M		X	X
1931	Oct	UCB 55213	Coconino	Winona, 19 km W	F			
1931	Nov	UCB 55212	Coconino	Gov't. prairie near parks	—			
COLORADO								
ca 1876	—	Unknown (n = 3)	—	"Vicinity of Denver"	—			
ca 1877	—	Unknown	Larimer	Valley of the Cache La Poudre	—			X
1878	Apr	AMNH 24412	El Paso	—	—			
1887	Feb	MCZ B4184	Larimer	—	M		X	X
1887	Jan 6	ANSP 8640	Larimer	—	F		X	X
1887	—	ANSP 8641	Larimer	—	—			
1888	Apr	DMNH 653	Grand	Middle Park	M			X
1900	Apr 1	UWZ 11776	El Paso	Colorado Springs	M		X	X
1904	—	Unknown	El Paso	Clyde Station	—			
1905	Jan 16	UCM 10658	Teller	Divide Station	M		X	X
1905	Apr 14	UCM 10659	Baca	N of Springfield	F		X	X
1905	Sep 23	UCM 10660	El Paso	Lake Moraine	F		X	X
1909	Jan 2	UCM-W59	Larimer	Laramie R., 19 km S of Wyoming border	M		X	
ca 1910	—	Private Collection	Rio Blanco	Meeker, 2 km	—			
ca 1910	—	Private Collection	Rio Blanco	Meeker, 2 km	—			
1910	Mar	UCM-W232	Weld	Cornish, 13 km E	—			X
1912	May 5	DMNH 257	Denver	Denver, Park Hill	(F)		X	
1913		CSU	Larimer	—	—			X
1914	Mar 15	DMNH 1208	Adams	Barr	F		X	X
1914	Dec 16	DMNH 1558	Adams	Simpson	M		X	X
1914	Dec 16	DMNH 1559	Adams	Simpson	F		X	
1915	Mar 30	AMNH 41994	Adams	Simpson	F		X	
1915	Oct 31	DMNH 5792	Jefferson	Semper	M		X	X
1916	Feb 21	DMNH 1684	Adams	Simpson	M		X	X
1916	Feb 21	DMNH 1883	Adams	Simpson	F		X	X
1919	Nov	USNM 234118	Saguache	Del Norte, 24 km NW	M		X	X
1922	—	USNM 265540	Weld	E of Greeley	—			X
1923	May 13	DMNH 1987	Weld	Grover, 8 km S	M		X	X
1923	May 13	DMNH 6726	Weld	Grover, 8 km S	F			X
1924	Feb	DMNH 2024	Baca	Furnace Canyon	M		X	X
1924	Feb	DMNH 2247	Baca	Furnace Canyon	(M)		X	X
1924	Feb	DMNH 2248	Baca	Furnace Canyon	(M)		X	
1926	Nov	USNM 247073	Park	Hartsel, 11 km S	F		X	X
1928	Feb 9	DMNH 2371	Baca	Furnace Canyon	(M)		X	
1930	Feb 11	DMNH 4322	Adams	Denver, 16 km E	F			X
1934	Aug	UCM-W493	Montezuma	Mancos	F		X	
1935	Jan 17	UCB 66019	Yuma	Wray	M	X	X	
1935	Dec 6	UCB 70209	Yuma	Wray	M	X	X	
1937	Nov 7	DMNH 3206	Weld	Greasewood	—			
1939	Sep 16	DMNH 3644	Denver	Denver, 1st and Holly	M		X	
1939	Aug	DMNH 3703	Denver	Denver	M			
1940	Aug 21	UCB 95039	Moffat	Craig, 35 km N	M			
1941	Jan	CMNH 19392	Moffat	Morapos Creek, 32 km SW Craig	—		X	X
1941	Oct 16	UCB 96904	La Plata	Durango	—			X
1941	Oct 16	UCB 96905	La Plata	Durango	—			X
1941	Dec 21	CMNH 20627	Moffat	Craig, 8 km W	M		X	X
1942	Jan	CMNH 20628	Moffat	Craig	F		X	X
1943	Apr 18	DMNH 5199	Chaffee	Buena Vista	M		X	
1946	Feb 10	AMNH 140397	Costilla	Ft. Garland–Buck Mountain	M	X	X	X
1951–52	Winter	Destroyed	Bent	Las Animas	—			
1952	Sep	Destroyed	Weld	Dearfield, 8 km E	—			
found 1977		CDOW 230	Logan	T10N R45W S21	—		X	
KANSAS								
ca 1877	—	Unknown	Wallace	Ft. Wallace	—			
1883	Nov 20	CU 4971	Trego	—	—			X
1884	Oct 10	USNM 188450	Trego	—	M		X	X

Other	Collecter	Citation	Meas- ured by us	Remarks
			X	Gunnison's prairie dogs
X-mount	W. S. Carlos (A. M. Alexander)			Gunnison's prairie dogs
	O. Wright (A. M. Alexander)			Gunnison's prairie dogs
				Gunnison's prairie dogs
X-mount	Mrs. M. H. Maxwell	Coues 1877		
	Dr. Law (through F. V. Hayden)	Coues 1877		
	S. N. Rhoads		X	
	C. K. Worthan (donated by S. N. Rhoads)			
	C. E. Aiken			White-tailed prairie dogs
X	C. E. Aiken	Cary 1911		
	E. R. Warren		X	2,806 m elevation; Gunnison's prairie dogs
	E. R. Warren		X	
	G. DeLong		X	3,126 m elevation; dead in lake (origin unk.)
		Warren 1910	X	White-tailed prairie dogs
X	R. S. Bull	Felger 1910; Warren 1910		R. S. Bull Collection, Meeker Hotel; white-tailed prairie dogs
X	R. S. Bull	Felger 1910; Warren 1910		R. S. Bull Collection, Meeker Hotel; white-tailed prairie dogs
	E. R. Warren			
X	C. Deardorff		X	Standing mount
	E. Sutton		X	
	W. W. Davidson		X	
X	W. W. Davidson		X	Standing mount
	J. B. Burns		X	
	W. D. Hollister		X	
	A. H. Burns		X	
	A. H. Burns		X	
			X	Gunnison's prairie dogs
	R. J. Niedrach		X	
	S. O. Singer		X	
	S. O. Singer		X	
	S. O. Singer		X	
			X	Gunnison's prairie dogs
	S. O. Singer			
	D. Spencer			
	O. W. Shirley		X	Gunnison's prairie dogs
	O. W. Shirley			
	R. Dietrich		X	Road kill
				Road kill
	A. E. Borell			White-tailed prairie dogs
	W. Dicus			White-tailed prairie dogs
	F. Barnes			Gunnison's prairie dogs
	F. Barnes			Gunnison's prairie dogs
	W. Dicus			White-tailed prairie dogs
	W. Dicus			White-tailed prairie dogs
	R. C. Prater		X	Gunnison's prairie dogs
	L. E. Miller		X	Gunnison's prairie dogs
		Cahalane 1954		Drowned in ditch.
		Cahalane 1954		Road kill
		Bissel 1979		
X-mount	L. H. Kerrick	Coues 1877		
				Not listed in Choate et al. 1982.
	A. B. Baker		X	

TABLE 6 continued.

Year	Date	Disposition	County	Site	Sex	Skel-eton	Crania	Skin
1885	Oct 20	USNM 15471/22427	Trego	—	F		X	X
1886	Apr 3	USNM 15470/22311	Trego	—	M		X	X
1886	Nov 20	USNM 188451	Trego	—	M		X	X
1887	Mar 31	USNM 188452	Trego	—	F		X	X
1887	Apr 3	USNM 188453	Trego	—	M		X	X
1887	Apr 5	USNM 188454	Trego	—	M			X
1887	Apr 5	USNM 188455	Trego	—	M		X	X
1887	Oct 17	AMNH 1203/1928	Trego	—	M		X	X
ca 1888	—	USNM 12299/22929	Wallace	Ft. Wallace	(M)		X	X
1888	—	USNM 188458	Trego	—	M	X	X	
1889	Apr 15	USNM 188456	Trego	—	F		X	X
1889	Apr	USNM 188457	Trego	—	F		X	X
1889	Nov	USNM 22537/30064	Trego	—	F		X	X
1890	May 8	USNM 22538/30065	Gove	—	M		X	X
1890	June 2	USNM 22539/30066	Gove	—	M		X	X
1891	Jan	USNM 25358/32771	Trego	Banner	F		X	X
1891	Feb 7	USNM 83992	Trego	Banner	M		X	
1891	Feb 4	USNM 83994	Trego	Banner	M		X	
ca 1891	—	USNM 19262/35376	Trego	—	M		X	X
ca 1891	—	USNM 19263/35016	Trego	—	M		X	X
1891	—	USNM 19294/35017	Trego	—	M		X	X
1891	—	USNM 19295/35018	Trego	—	M		X	X
1891	—	USNM 34977	Trego	—	M		X	X
1891	—	USNM 35011	Trego	—	F	X	X	X
1891	Mar 6	USNM 83993	Trego	Banner	F		X	X
1891	—	USNM 19538	Trego	—	M			X
1896	Nov 24	KUMNH 1487	Kingman	Kingman	M		X	X
1901	Nov 2	USNM 110772	Logan	Oakley	M		X	
1904	Dec	UCM 895	Saline	—	M			
1905	—	MCZ 42723	Trego	Wakeeney	(M)		X	X
1909	—	to USNM (no record) (NZP 7494)	Wallace	—	F			
1910	—	USNM 199737 (NZP 7802)	Wallace	—	F		X	
1910	—	Destroyed (NZP 7804)	Wallace	—	—			
1910	—	Unknown (NZP 7803)	Wallace	—	—			
1910	—	London Zoo (NZP 7805)	Wallace	—	—			
1914	May	SDNHM 6720	Decator	—	F			X
1914	Sep	KUMNH 134415	Trego	Banner	M		X	X
1930	Fall	KUMNH 10177	Lincoln	Lucas	M		X	X
1933	Oct	KUMNH 11077	Hamilton	Coolidge	M	X	X	X
1935	Jan 24	MCZ 43727-KU 10973	Hamilton	Coolidge	M	X	X	
1935	Jan	KUMNH 12119	Hamilton	Coolidge	M	X	X	X
1939	—	CM 21391	Jewell	Ionia	M			
1944	Oct	HM 25099	Smith	S of Invale, Neb.	M			
1957	Dec 31	KSU	Sheridan	Studley	M		X	X
found 1978	—	MHP 15569	Gove	Healey, 13 km NW	—		X	

MONTANA

Year	Date	Disposition	County	Site	Sex	Skel-eton	Crania	Skin
ca 1877	—	Unknown	—	"Milk River"	—			X
1892	Aug	ANSP 8041	Cascade	Great Falls	F		X	
1910	Jan	USNM 155475	Dawson	Glendive	(M)		X	X
1915	—	SCZ MUNICH	Garfield	Jordan	M		X	
1915	—	FMNH 25621	Garfield	Jordan	—	X		
1915	—	FMNH 25622	Garfield	Jordan	M	X		
1915	—	FMNH 25623	Garfield	Jordan	—		X	
1916	May	MSU 369	Custer	—	M	X	X	
1916	Sep 23	UCB 25709	Garfield	Jordan, 6 km S	M	X	X	X
1916	Sep	USNM 224450	Custer	Kimball	M		X	X
1916	Sep 23	AMNH 40078	Garfield	Jordan, 6 km S	M		X	
1919	May	USNM 232400	Rosebud	NW Calabar, Whitetail Creek	M		X	X
1920	Jan	USNM 239138	Teton	Choteau	(M)		X	X
1920	Apr	USNM 234970	Powder River	Broadus	F		X	X
1920	Apr	USNM 234971	Powder River	Broadus	F		X	X

Other	Collector	Citation	Meas-ured by us	Remarks
	A. B. Baker		X	
	A. B. Baker		X	
	A. B. Baker		X	
	A. B. Baker		X	
	A. B. Baker		X	
	A. B. Baker		X	
	A. B. Baker		X	
	A. B. Baker		X	
	L. H. Kerrick		X	NZP specimen; (no accession card) from NZP to USNM 22 May
	A. B. Baker		X	
	A. B. Baker		X	
	A. B. Baker		X	
	A. B. Baker		X	
	A. B. Baker		X	BSC
	A. B. Baker		X	BSC
	C. A. Hawkes		X	
	L. W. Purington		X	
	L. W. Purington		X	NZP (no accession card), rec'd. 19 Feb by USNM
			X	NZP (no accession card), rec'd. 19 Feb by USNM
			X	NZP (no accession card), rec'd. 24 Feb by USNM
			X	NZP (no accession card), rec'd. 24 Feb by USNM
			X	NZP (no accession card), rec'd. 19 Feb by USNM
			X	NZP (no accession card), rec'd. 19 Feb by USNM
	L. W. Purington		X	
	A. B. Baker			
			X	
	W. H. Osgood		X	BSC
X-mount	E. H. Herrick (L. H. Kerrick?)		X	
				NZP rec'd. 3 Apr 1909; died Nov 2 1911
			X	NZP rec'd. 17 Jun 1910; died 2 Jul 1915
	H. Byxbe			
				NZP rec'd. 17 Jun 1910; died 26 Nov 1913
				NZP rec'd. 17 Jun 1910
				NZP rec'd. 17 June 1910; exchanged 2 Feb 1911
	R. Kellogg		X	
	O. Conrad		X	
	D. Conard (O. Conrad?)		X	Permanent loan to MCZ 4 Jan 1949
				Missing
X-mount		Choate and Fleharty 1975		"Iona"; body mount
	C. Karnes	Taylor 1961 Boggess et al. 1980		
	C. Cavilieer	Coues 1877		
	R. Williams (donated by S. N. Rhoads)		X	
X-mandible	L. L. Walters	P. Youngman, pers. comm.		From FMNH
	Parker & Wells			Skin missing Apr 1980
	L. L. Walters		X	
			X	
	L. L. Walters		X	ADC Reports
			X	
			X	
			X	

TABLE 6   continued.

Year	Date	Disposition	County	Site	Sex	Skel-eton	Crania	Skin
1920	May	USNM 234972	Powder River	Broadus	F		X	X
1920	May	USNM 234973	Powder River	Broadus	M		X	X
1920	Oct	Unknown	Rosebud	Ashland	—			
1923	Sep	USNM 243818	Rosebud	Birney	M		X	X
1923	Sep	USNM 243819	Rosebud	Birney	F		X	X
1923	Oct	USNM 243820	Powder River	Ashland, E	F		X	X
1923	Nov	Unknown	Rosebud	Lee	—			
1923	Nov	USNM 243909	Bighorn	St. Xavier	F		X	X
1923	Nov	USNM 243910	Bighorn	St. Xavier	(M)		X	X
1923	Nov	Unknown	Rosebud	Ashland	—			
1923	Nov	Unknown	Rosebud	Ashland	—			
rec'd 1923		USNM X 23272	Bighorn	Crow Agency	—			X
1923	Dec	Unknown	Powder River	Camps Pass	—			
1923	Dec	Unknown	Phillips	Phillips	—			
1924	Jan	Unknown	Phillips	Regina	—			
1924	Sep	Unknown	Choteau	Geraldine	—			
1928	Aug	Unknown	Prairie	Terry	—			
1928	Aug	Unknown	Prairie	Terry	—			
1935	Sep	UCB 78134	Carter	—	M	X		
1942	Jan	USNM 288288	Fergus	Harlowtown, 48 km N	—			X
1944	Oct	KU 14411	Carter	—	M	X	X	X
1948	Sep	Destroyed	Golden Valley	Lavina, 8 km S	M			
1949	Mar	MSU 370	Yellowstone	Billings, 16 km SE	M		X	X
1952	—	Unknown	Rosebud	Ingomar	M		X	
1953	Nov	USNM 287322	Carter	Alzada, 11 km N	M			X
found 1983		BSC	Blaine	Ft. Belknap Reservation T30N R25E S17	—		X	
found 1984	Jan	MDFWP 2344	Carter	Ekalaka	(M)			
found 1984	Jan	MDFWP	Carter	Ekalaka	—			
—	—	USNM 13113/21976	Bighorn	Ft. Custer	(M)		X	X
NEBRASKA								
ca 1877	—	USNM 14580	—	—	(M)	X	X	
1890s	—	Private Collection	Frontier	Curtis	—			
1890s	—	Private Collection	Frontier	Curtis	—			
1890s	—	Unknown	Lancaster	Lincoln	—			
ca 1890s	—	UNZM 2333	Box Butte	Marsland, 8 km SE	—		X	
1917	Sep	AMNH 42567	Sioux	Agate	M		X	
1919	May	Brookings 1989	Frontier	Maywood	—			
1927	—	HM 10038a	Buffalo	Gibbon	—			
1934	Mar 10	AMNH 121610	Webster	Rosemont	M		X	X
1938	Jan 26	HM 18041	Clay	Glenvil	—			
1938	—	Unknown	Custer	Anselmo	F			
1939	Apr 16	HM 19074	Furnas	Cambridge	—			
1946	May 6	UNZM 3323	Banner	Gering, 14 km S	F			X
1947	—	Destroyed	Knox	—	—			
1949	Mar 16	NGFP	Phelps	Overton, S. Platte River	—			
—	—	Private Collection	Garden	Oshkosh	—			
—	—	Brookings 10038b	Buffalo	Gibbon	—			
—	—	Unknown	Buffalo	Kearney	—			
—	—	Unknown Private Coll.	Hamilton	Harvard, N	—			
—	—	Private Collection	Buffalo	Kearney	—			
—	—	Unknown	Custer	Arnold	—			
—	—	USNM 12387	Lincoln	N Platte			X	
—	—	USNM 12409	Dawes	Spotted Tail Agency				X
NEW MEXICO								
found 1899	Jun	USNM	Chaves	Roswell	—			
1915	Mar 18	YPM 1969	Catron	Reserve, 24 km N	M		X	X
1918	May 1	USNM 228789	McKinley	San Mateo, 16 km NE	M		X	X
1918	Oct 25	USNM 231363	Cibola	Bluewater, 3 km N	M			X

Other	Collector	Citation	Measured by us	Remarks
			X	ADC Reports
			X	
		D. L. Flath, pers. comm.		ADC Reports
			X	
			X	
			X	
		D. L. Flath, pers. comm.		ADC Reports
			X	
			X	
		D. L. Flath, pers. comm.		ADC Reports
		D. L. Flath, pers. comm.		ADC Reports
		D. L. Flath, pers. comm.		ADC Reports
		D. L. Flath, pers. comm.		ADC Reports
		D. L. Flath, pers. comm.		ADC Reports
		D. L. Flath, pers. comm.		ADC Reports
		D. L. Flath, pers. comm.		ADC Reports
		D. L. Flath, pers. comm.		ADC Reports
	M. W. Jellison			
			X	
	Crabb & Watson	Crabb & Watson 1950		Road kill
	Crabb & Watson	Cahalane 1954 (#10)		
X-baculum		Hoffman et al. 1969:597		
	C. Knowles			
	S. Forrest			
X-mandible	T. M. Campbell III			
			X	
		Coues 1877	X	
		Fichter & Jones 1953 (#4)		Rees Heaton Collection; present disposition unk.
		Fichter & Jones 1953 (#4)		Rees Heaton Collection; present disposition unk.
	L. Bruner	Fichter & Jones 1953 (#1)		
X		Fichter & Jones 1953 (#3)		
	A. Thompson		X	
	C. J. Pfeifer	Fichter & Jones 1953 (#9)		To HM; to Hastings College; present disposition unknown
X-mount	J. Shields	Fichter & Jones 1953 (#10)		
	H. Turner	Fichter & Jones 1953 (#14)	X	
	Stahnke	Fichter & Jones 1953 (#11)		To HM; to Hastings College; present disposition unknown
X-mount		Velich 1961		
		Fichter & Jones 1953 (#13)		To HM; to Hastings College; present disposition unknown
		Fichter & Jones 1953 (#17)		
	R. Block	R. Block, pers. comm.		Trapped
X-mount		Fichter & Jones 1953 (#18)		Road kill
	M. Maryott	Fichter & Jones 1953 (#15)		
		Fichter & Jones 1953 (#12)		To HM; to Hastings College; present disposition unknown
		Fichter & Jones 1953 (#5)		
	W. Townsley	Fichter & Jones 1953 (#6)		
	O. Blevins	Fichter & Jones 1953 (#7)		Kearney Public School
		Fichter & Jones 1953 (#16)		
		Fichter & Jones 1953 (#2)		
X-mandible	V. Bailey (BSC)	Bailey 1932		Formerly confused as Santa Rosa, Guadalupe Co., 1903, now believed to be misstated and is Roswell; BSC
	J. S. Ligon (BSC)			Gunnison's prairie dogs; skin measured
	J. S. Ligon (BSC)		X	Gunnison's prairie dogs
	C. P. Musgrave (BSC)			Gunnison's prairie dogs

TABLE 6 continued.

Year	Date	Disposition	County	Site	Sex	Skel-eton	Crania	Skin
1918	Mar 22	USNM 230773	Catron	Magdalena, 75 mi SW	F			X
1925	Nov 14	YPM 1970	Bernallio	Albuquerque, 12th St.	M			X
1929	Apr 7	ANSP 14509	Lincoln	Picacho, 5 km S	M		X	X
1929	Dec 8	BSC 1210	Colfax	Moreno Valley, Aqua Fria	F		X	
1930	Aug 13	KU 7146	Santa Fe	Santa Fe, 13 km SW	M	X	X	X
1934	Oct 20	USNM 251453	McKinley	Gallup	(F)		X	X
1937	—	Unknown	Cibola	El Moro National Monument	—			X
1940	—	Unknown	McKinley	Mexican Springs	—			
1954	—	Destroyed	Lea	Lovington, 17 km N	—			

NORTH DAKOTA

Year	Date	Disposition	County	Site	Sex	Skel-eton	Crania	Skin
1912	—	Unknown	Morton	Ft. Rice	—			
1913	Jun 20	USNM 201945	Dunn	Quinion between Killdeer & Medora	F		X	
1915	—	Unknown	Mercer	Stanton	—			
1927	Aug	NDSHS 4173	Golden Valley	Beach	—			
1933	Winter	NDSHS 5159	Slope	Marmarth	—			
1951	Mar 5	NDSHS	Hettinger	Mott, 2 km S	—			
1954	—	NDSHS 13063	—	—	F			
1954	Dec	UM 103451	Sioux	Morristown, S. Dak., 10 km N	M		X	X
found 1980		UND	Billings	SE	—		X	

OKLAHOMA

Year	Date	Disposition	County	Site	Sex	Skel-eton	Crania	Skin
1923	Sep	USNM 243787	Cimarron	—	—		X	
1924	Jul	OKSU 9266	Texas	Adams, 13 km SE	F			
1928	Jul 25	OU 2211	Cleveland	Norman, 2 km E	—			X
1932	Winter	Destroyed	Texas	22 km S Kansas line	—		X	
—	—	NSCM 858	Woods	Hopeton	—			

SOUTH DAKOTA

Year	Date	Disposition	County	Site	Sex	Skel-eton	Crania	Skin
1889	—	Unknown	Shannon	Pine Ridge Agency	—			X
early 1900s	—	MHM	Pennington	—	M			
early 1900s	—	MHM	Pennington	—	F			
1905	Spring	Unknown	Hand	T109N R70W S26, Bailey	—			
1905	Spring	Unknown	Hand	T109N R70W S26, Bailey	—			
1905	Spring	NYZP-AMNH 22894	Hand	T109N R70W S26, Bailey	M		X	
1905	Spring	NYZP	Hand	T109N R70W S26, Bailey	—			
1905	Winter	Unknown	Bennett	Across line from Merriman, Neb.	—			
1913	—	WHO J23	Pennington	Box Elder	—			
1915	Aug	USNM 209150	Mellette	White River	M			X
1920	Oct 4	Destroyed	Jackson	Interior	M			
1921	Feb	Destroyed	Pennington	Scenic	M			
1922	Mar	Unknown	Custer	Wind Cave National Park	—			
1923	Sep 16	USNM 243799	Shannon	Pine Ridge	(F)		X	X
1923	Nov 1	USNM 243990	Harding	Govert	M		X	X
1924	—	Unknown (n = 3)	—	—	—			
1924	Sep	Unknown	—	—	—			
1924	Oct	Unknown (n = 6)	—	—	—			
1925	—	Unknown (n = 6)	—	—	—			
1925	Mar	Unknown (n = 2)	—	—	—			
1925	Jul	Unknown	—	—	—			
1925	Aug	Unknown	—	—	—			
1925	Sep	Unknown	—	—	—			
1925	Nov	USNM 241014	Shannon	Pine Ridge	F		X	
1925	Dec 24	AMNH 70590	Pennington	Scenic	M	X	X	
1926	—	Unknown	—	—	—			
1927	—	Unknown (n = 2)	—	—	—			
1927	Mar	Unknown (n = 2)	—	—	—			
1927	Apr	Unknown (n = 2)	—	—	—			

Other	Collecter	Citation	Measured by us	Remarks
	J. S. Felkner			Gunnison's prairie dogs
	J. S. Ligon (BSC)			Gunnison's prairie dogs; skin measured
	W. Huber			Skin measured
	Aldous (BSC)	Aldous 1940	X	Skin measured; Gunnison's prairie dogs; kept captive 5 months
	T. E. White		X	Skin measured; Gunnison's prairie dogs
	M. E. Musgrave (BSC)		X	Gunnison's prairie dogs
	J. Brewer	Fortenbery 1971; "probable" Hubbard & Schmidt 1984		Skin made but lost; drowned in pools; Gunnison's prairie dogs
X	W. E. Fair	Halloran 1964; "highly probable" Hubbard & Schmidt 1984		Road kill; fluid specimen made but lost
X-mount	J. Richardson	"probable" Hubbard & Schmidt 1984		Mount made but subsequently destroyed
	H. Eaton	Bailey 1926		To Ag College, Fargo
	S. G. Jewett		X	BSC
X-mount	Kellogg	Bailey 1926		
X-mount	H. L. Rice			
X-mount	J. H. Cramer			Received 13 Jun 1935
X-mount				
X-mount				
X	A. Freidt			
	R. Crooke			
X-mount				
	F. Barkley			
		Hibbard 1934		
X-mount				
	A. B. Baker	Henderson et al. 1969 (#1)		ADC records
X-mount	H. Behrens			H. Behrens Collection
X-mount	H. Behrens			H. Behrens Collection
X-mount		Moon 1905; Henderson et al. 1969 (#6)		
X-mount		Henderson et al. 1969 (#6)		
		Henderson et al. 1969		Sold alive
		Henderson et al. 1969 (#6)		Sold alive; probably sold to NYZP, rec'd 2 BFFs Oct 1905; further at least one of these became AMNH 22894, 1 Jun 1906
X-mount		Henderson et al. 1969 (#7)		ADC records, trapped.
X-mount		Henderson et al. 1969 (#10)		
	R. A. Ward			
	B. Darymple	Henderson et al. 1969 (#13)		ADC records, trapped
	B. Darymple	Henderson et al. 1969 (#14)		ADC records, trapped
		Lovaas 1973		Trapped by ADC and killed
	D. P. Stearns	Linder et al. 1972	X	Captured by D. P. Stearns, BSC, Sep 1923 (Linder et al. 1972); to NZP (cat 11.281) 19 Sep; died 4 Nov 1925; to USNM
	L. Knowles			
		Linder et al. 1972		
		Linder et al. 1972		Trapped ADC
		Linder et al. 1972		Trapped ADC
		Linder et al. 1972		
		Linder et al. 1972		Poisoned
		Linder et al. 1972		Trapped
		Linder et al. 1972		Trapped
		Linder et al. 1972		Trapped
			X	
	R. E. Lemley		X	
		Linder et al. 1972		
		Linder et al. 1972		
		Linder et al. 1972		Trapped
		Linder et al. 1972		Trapped

TABLE 6 continued.

Year	Date	Disposition	County	Site	Sex	Skel-eton	Crania	Skin
1927	Aug	Unknown	—	—	—			
1927	Sep	AUG	Pennington	Rapid City, 29 km S	F			
1927	Winter	WHO J155	Pennington	Conata	—			
1928	Feb	Unknown	—	—	—			
1928	Mar	Unknown (n = 5)	—	—	—			
1928	May	Unknown	—	—	—			
1928	Aug 13	SDNHM 17538	—	—	F			X
1928	Aug 13	SDNHM 17539	—	—	M			X
1928	Aug 13	SDNHM 17540	—	—	M		X	X
1929	May 10	SDNHM 17537	—	—	M			X
1931	Dec 31	UNZM 4451	Custer	Hermosa	M		X	X
1946	Nov	ISU 33434	Lyman	—	M			X
1950	Dec 8	USNM 285877	Dewey	Isabel, 19 km S	M		X	
1952	Oct 23	UMMNH 3667	Perkins	Zeona, N	F	X		
1953	Dec	USNM 287371	Pennington	Conata Basin	F	X	X	X
1953	Aug	USNM (no record)	Haakon	T1N R24E	F			
1953	Aug	Unknown	Haakon	T1N R24E	M			
1953	Aug	Released WCNP	Haakon	T1N R24E	M			
1953	Aug	Released WCNP	Haakon	T1N R24E	M			
1953	Aug	Released WCNP	Haakon	T1N R24E	F			
1954	Mar	Unknown	Stanley	Midland, 24 km N	M			
1956	Summer	Private Collection	Lake	Madison	—			X
1958	Jan	Private Collection	Ziebach	Faith, 8 km SE	M			X
1958	Summer	Destroyed	Lyman	Reliance, 3 km W	M			
1959	—	Destroyed	Mellette	White River, 16 km S	M			
1959	Fall	SDGFP	Sully	Agar, 19 km W	M			
1960	Summer	DMNH	Washabaugh	T41N R35W	M			
1960	Oct 22	USNM 348132	Sully	Onida, 14 km W	M			
1961	Aug	SDSU 110	Lyman	Reliance, 5 km N	M			
1963	Dec	Destroyed	Mellette	T40N R30W, 24 km SW White River	—			
1964	Sep	SDSU 149	Tripp	T40N R78W	—			X
1964	Oct 7	BNP	Washabaugh	T41N R37W, Wanblee	M			
1965	Aug	SDSU 186	Mellette	T40N R32W	M		X	
1965	Sep 29	SDSU 187	Haakon	T2N R19E	F			X
1965	Oct 10	SDSU 190	Jackson	T2S R20E, 14 km W Kadoka	M			X
1966	Sep	USNM 289498	Mellette	White River	F		X	
1966	Mar	KUMNH 121795	Todd	T38N R26W	M	X		
1967	Apr 29	SDSU 212	Bennett	T37N R39W	F		X	
1967	May 16	SDSU 215	Jones	T3S R29E	F		X	
1967	Sep 12	SDSU 224	Mellette	White River, 5 km W	M			
1971	Fall	PAT	Mellette	—	F			
1971	Fall	PAT	Mellette	—	F			
1971	Fall	PAT	Mellette	—	F			
1971	Fall	PAT	Mellette	—	F			
1971	Fall	Private Collection	Mellette	—	M			
1971	Fall	PAT	Mellette	—	M			
1972		PAT	Mellette	—	F			
1973		PAT	Mellette	—	M			
1973		PAT	Mellette	—	F			
—	—	USNM 122620	Hughes	Pierre	(M)		X	
TEXAS								
1882	—	Unknown	Taylor	Abilene	—			
1885		USNM 15018	Cooke	Gainesville	—			X
1886	—	ROM 19-11-1-47	—	Rio Grande	—		X	X
1886	—	USNM 188459	Cooke	—	M			X
found 1894	May	USNM 65061	Childress	Childress	(M)		X	
1901	—	ANSP 11842	Baylor	Seymour	F		X	X
prior to 1902		Destroyed	Crane	Grand Falls				
1902	Summer	Unknown	Lipscomb	Lipscomb	—			X
1905	—	ANSP 12143	Baylor	Seymour	M			X

Other	Collector	Citation	Meas-ured by us	Remarks
		Linder et al. 1972		Trapped
X-mount	H. Behrens			
	T. Bennett			
		Linder et al. 1972		Trapped
		Linder et al. 1972		Trapped
		Linder et al. 1972		Trapped
		Linder et al. 1972		ADC capture; specimen in tally from 1928
		Linder et al. 1972		ADC capture; specimen in tally from 1928
		Linder et al. 1972		ADC capture; specimen in tally from 1928
		Linder et al. 1972		ADC capture; specimen in tally from 1929
X	F. M. Dille			
	A. Lester			
	R. Block		X	ADC
X-mount	A. Hinds			
			X	
	G. Barnes	Garst 1954		Carcass frozen to USNM; no record. ADC
	G. Barnes	Garst 1954		Died in captivity, skull only saved. ADC
	G. Barnes	Garst 1954		ADC
	G. Barnes	Garst 1954		Captive until Dec 1953. ADC
	G. Barnes	Garst 1954		
	B. A. Nelson	Henderson et al. 1969 (#56)		
		Henderson et al. 1969 (#68)		
	D. Capp	Henderson et al. 1969 (#82)		
	R. F. Wahlin	Henderson et al. 1969 (#83)		Road kill
	T. Johnson	Henderson et al. 1969 (#90)		Shot
X-mount	O. VonWald			
X-mount	W. Allen	Henderson et al. 1969 (#103)		Through Glen Titus
X-mount	D. Badger & T. Lockwood			
X-mount	C. F. Anderson	Progulske 1969		Died in captivity
		Henderson et al. 1969		R. Adrian observed. Shot
	G. Johnson			Shot
X-mount		Henderson et al. 1969 (#155)		Viscera at SDSU. Shot
	O. Huber			Trapped
	R. Henderson			Killed by ranch dog
	R. Henderson			Road kill
			X	Carcass to SDSU. Shot
	W. Abbot	Henderson et al. 1969 (#196)		Listed in private collection in Henderson et al. 1969. Killed by dogs
X-carcass	J. Milk			Road kill
X-carcass	D. Richardson			Road kill
	J. Krogman			Road kill
X-carcass				Juvenile, died of distemper vaccine
X-carcass				Juvenile, died of distemper vaccine
X-carcass				Juvenile, died of distemper vaccine
X-carcass		Carpenter, pers. comm.		Juvenile, died 1971 of distemper vaccine
X-carcass		Carpenter, pers. comm.		Juvenile, captive 6 years, died 1978; to Meeteetse Bank Apr 1982
X-carcass		Carpenter, pers. comm.		Captured as juvenile, captive 4 years, died 1976
X-carcass		Carpenter, pers. comm.		Captured as juvenile, died Oct 1978
X-carcass		Carpenter, pers. comm.		Adult, died Apr 1979
X-carcass		Carpenter, pers. comm.		Adult, died Jan 1979
			X	
	F. J. Thompson	Coues 1882		Captured live; held at Cincinnati Zoo
	G. H. Ragsdage	True 1885		
			X	
				Captive Philadelphia Zoo 27 Apr 1901–2 Sep 1903; accession to ANSP 5 Jan 1904; Zool. Soc. Philadelphia
		Bailey 1905		
		Bailey 1905		
				Zool. Soc. Phila., received 14 Aug 1905, died 27 Nov 1905; accession ANSP 1905

TABLE 6 continued.

Year	Date	Disposition	County	Site	Sex	Skel-eton	Crania	Skin
1905	—	Private Collection	Baylor	Seymour	F			
1933	Dec	UCM 5263	Lubbock	Lubbock	M		X	
1934	Feb	UCM 5287	Lubbock	Lubbock	M		X	
1934	Dec 21	UM 76971	Lubbock	Slide, 5 km SW	M		X	X
UTAH								
1937	Apr 21	UCB 77840	San Juan	Blanding, 3 km S	M			
WYOMING								
1851	—	USNM	Goshen	Ft. Laramie	—			X
ca 1877		Unknown	Laramie	Cheyenne Depot	—			
1883	Dec	USNM 13996/21066	Laramie	Cheyenne, 19 km on Duck Creek	—		X	
1895	May	USNM 71750	Weston	Newcastle	F			X
1910	May	USNM 168741	Weston	Newcastle	(M)		X	
1911	Spring	USNM 180719	Crook	Beulah	M			X
1911	Oct	USNM 180718	Johnson	Clear Creek, above Big Red (Ucross)	—			X
1916	Apr	USNM 211513	Niobrara	Manville	M		X	
1916–1928		Unknown (n = 10)	—	—	—			
1917	Sep	USNM 227703	Converse	Douglas	M			X
1924	Oct	USNM 245641	Albany	Laramie, 8 km W	M		X	X
ca 1930	—	Private Coll. (n = 2)	Park	—	—			X
1935		Private Collection	Sheridan	Leiter, 22 km N	M			X
1939	Nov	Private Collection	Albany	Eagle Park, W of Laramie Peak	—			X
ca 1946	—	Unknown	Sweetwater	Wamsutter and Rock Springs	—			X
1950	—	Destroyed	Albany	Laramie, 2 km W	—			
1955	—	UW	Albany	Laramie	—			
1981	Sep 26	BSC 7934	Park	Meeteetse	M	X	X	X
1982	Mar	BSC (Biota #11)	Park	Meeteetse	M	X	X	X
1982	Spring	BSC (Biota #1)	Park	T48N R102W S17	(F)		X	
1982	Winter	BSC 10481	Park	Meeteetse	M	X	X	X
1983	Aug	WGF (Biota #16)	Park	Meeteetse	—	X	X	X
1983	Winter	WGF (Biota #14)	Park	T48N R102W S18	M			
1983	Oct	BSC	Park	T48N R102W S4	F			
1983	Dec	USFWS	Park	T48N R102S S7	M		X	
1984	Winter	WGF	Park	T48N R102W S8	F			
1984	Sep	BSC	Park		M		X	
1984	Sep	BSC	Park		F			
found 1978		BSC	Carbon	T22N R77W S31, S Medicine Bow	(M)		X	
found 1978	Aug 15	BSC 4059	Uinta	T16N R117W S7	(F)		X	
found 1979		WGF	Converse	T41N R70W S32, Rosecrans	—		X	
found 1979		BSC 4442	Unita	T16N R118W S12	(F)		X	
found 1979		BSC 4548	Carbon	T23N R80W S18	(F)		X	
found 1979	Sep 5	BSC 4547	Carbon	T23N R81W S2, 13 km NE Hanna	—		X	
found 1979	Sep 11	BSC 4441	Unita	T16N R118W S1	—		X	
found 1979		BSC 4342	Carbon	T23N R84W S34	(F)		X	
found 1981	Aug 27	BSC 7558	Sweetwater	T22N R93W S33, 19 km N Wamsutter	(F)		X	
found 1982	Spring	BSC (Biota #10)	Park	Meeteetse	(M)	X	X	X
found 1982	Mar 15	BSC (Biota #4)	Park	T48N R102W S8	(F)			
found 1982	Apr 20	BSC (Biota #5)	Park	T48N R102W S7	(M)		X	
found 1982	Apr 23	BSC (Biota #6)	Park	T48N R102W S8	—		X	
found 1982	Jun 9	BSC (Biota #7)	Park	T49N R102W S31	(F)		X	
found 1982	Jun 26	BSC (Biota #9)	Park	T48N R103W S2	(M)		X	
found 1982	Aug 9	BSC (Biota #3)	Park	T48N R102W S7	(F)		X	
found 1982	Sep 22	BSC (Biota #14)	Park	T48N R103W S2	(F)		X	
found 1982	—	WGF	Park	Meeteetse	M	X	X	X
found 1982	—	WGF	Park	Meeteetse	M	X	X	X
found 1983		WGF (Biota #15)	Park	T48N R102W S7	—			
found 1984	Apr 8	BSC	Park	Meeteetse				
found 1984	Spring	WGF	Park	Meeteetse			X	

Other	Collecter	Citation	Meas- ured by us	Remarks
				D. White from ZSP, received 14 Aug 1905, died 28 Feb 1906
	D. Spencer		X	
	D. Spencer		X	
	P. A. Burns			Gunnison's prairie dogs
	A. Culbertson	.udubon & Bachman 1851		Destoyed by 1872 (Coues 1872).
X-mount	Capt. J. Gillis	Coues 1877		
	J. Mason and C. Ruby		X	
	F. Bond			
	S. E. Piper		X	
			X	
	US Biological Survey	Day & Nelson 1928		Killed 10 in predator trapping
				White-tailed prairie dogs
	B. Edgar	Clark 1975		
		Clark 1975		
		Clark 1975		
	P. Muchmore	Clark 1975		Road kill; formerly in WGF collection; white- tailed prairie dogs
	R. W. Fautin			Road kill
	R. W. Fautin			Stolen; white-tailed prairie dogs
	L. Hogg		X	Hogg Ranch kill; white-tailed prairie dogs
	J. Renner			Road kill; white-tailed prairie dogs
	L. Richardson		X	White-tailed prairie dogs
	T. W. Clark		X	Starved in burrow; white-tailed prairie dogs
	T. W. Clark			Juvenile; white-tailed prairie dogs
X-carcass	M. Karl			Young of year; white-tailed prairie dogs
X-carcass	D. E. Biggins		X	Killed by predator; young of year; white-tailed prairie dogs
X-carcass	D. E. Biggins			Adult, killed by predator; white-tailed prairie dogs
X-carcass	J. Hasbrouck			Adult; white-tailed prairie dogs
X-partial crania	D. E. Biggins			Partial cranium; killed by predator; juvenile; white-tailed prairie dogs
X-mandibles	V. Semonsen			Killed by predator; juvenile; white-tailed prairie dogs
	T. M. Campbell III	Clark and Campbell 1981	X	Adult; white-tailed prairie dogs
		Martin & Schroeder 1978		1/2 skull
	J. Bridges			
	V. Jameson	Martin & Schroeder 1979	X	White-tailed prairie dogs
		Martin & Schroeder 1979	X	White-tailed prairie dogs
	D. Higgins	Martin & Schroeder 1979		1/2 skull; white-tailed prairie dogs
	S. Martin	Martin & Schroeder 1979	X	White-tailed prairie dogs
		Martin & Schroeder 1979	X	White-tailed prairie dogs
	S. Martin		X	White-tailed prairie dogs
	L. Richardson			Full head (eagle); white-tailed prairie dogs
	T. W. Clark		X	Adult; white-tailed prairie dogs
	J. Grenier		X	Adult; white-tailed prairie dogs
X-mandibles	T. W. Clark		X	Subadult; white-tailed prairie dogs
	S. C. Forrest		X	Adult; white-tailed prairie dogs
	L. Richardson		X	Subadult; white-tailed prairie dogs
	L. Richardson		X	Adult; white-tailed prairie dogs
	L. Lee		X	Adult; white-tailed prairie dogs
	T. Thorne			Trap kill; white-tailed prairie dogs
	T. Thorne			Trap kill; white-tailed prairie dogs
X-mandibles	T. W. Clark			White-tailed prairie dogs
	T. Taylor		X	White-tailed prairie dogs
	B. Phillips			White-tailed prairie dogs

TABLE 6 continued.

Year	Date	Disposition	County	Site	Sex	Skel-eton	Crania	Skin
SASKATCHEWAN								
1924	Sep 30	SMNH 1588	—	Regina, 6 km SE	M			
1930	Feb	NMC 11693	—	Shaunavon	—			X
1931	Dec 20	SMNH 3183	—	Gergovia, S35 T2 R24	F			X
1932	—	NMC from SMNH 2965	—	Big Beaver, S5 T2 R24	—			X
1932	Dec 1	NMC 11703	—	Frontier	—			X
1932	Dec 21	NMC 11700	—	Shaunavon, 32 km SE	F	X		X
1932	Dec 28	NMC 11752	—	Climax, S33 T3 R18	M	X		X
1933	Jan	NMC 11744	—	Shaunavon	M			X
1933	Jan 6	SMNH 3168	—	Climax	—			X
1933	Apr	SMNH 3186	—	Expanse, 8 km N	—		X	X
1934	Nov 23	NMC 12682	—	Shaunavon	M		X	X
1935	Nov 20	NMC 14078	—	Senate	M		X	X
1935	Nov	NMC 14095	—	Wood Mountain	M	X		X
1935	Dec 5	NMC 14079	—	South Fork, 19 km N	M	X		X
1935	Dec 4	SMNH 3656	—	Keeler, S22 T19 R29	—			
1935	Dec	SMNH 3657	—	Hazlet	—			
1937	Dec 7	NMC 24235	—	Climax, 11 km N	F			X
—	—	ROM 33–5–23–2	—	Maple Creek	F	X		X
—	—	SMNH 11441	—	—	—			X
—	—	SMNH 11442	—	—	—			X
ALBERTA								
1901	May	FMNH 8207	—	Gleichen	F		X	X
ADDITIONAL REPORTS								
1888		AMNH 2546			—		X	
1903		AMNH 22820-NYZ 02699			M	X	X	X
1928		NYZ 02701			—			X
1928		NYZ 02700			—			X
1920s		Syracuse (n = 3)						X
1934		ZSP						
1934		ZSP						
prior to 1862	May	MCZ 14947						
		BSC 4282			(F)		X	
		BSC 4283			M		X	
		USNM 35087			M			
		USNM 35088			M	X		
—		BMS			—			X
		FMNH						X
		AMNH 35041			M	X		
ca 1877		USNM 11932						
MISSOURI								
1876		USNM 21965		Licks's River	(F)		X	

COLORADO

Fifty-four specimens of ferrets are listed from Colorado (Table 6, Fig. 11), including 47 specimens in museums and an additional 7 verified specimens whose present dispositions are unknown. Armstrong (1972) examined 30 specimens from Colorado and listed an additional 27 records, many of which were sight records only.

The earliest known verified specimen is AMNH 24412, collected in 1878 in El Paso County. Coues (1877), however, mentioned several accounts of black-footed ferrets from Colorado and had at least two occasions to examine specimens from there. One was a specimen in "defective" condition shot in "the valley of the Cache La Poudre River, near the northern border of Colorado" (Larimer

Other	Collecter	Citation	Measured by us	Remarks
X-mount	C. Pickett			
				Not in collection—missing
	H. F. Hughes			
	H. F. Hughes			
	J. Prochazka			
				Missing
				Missing
	C. Guiguet			
	W. Klym			
	H. F. Hughes			
X-mount				
X-mount	F. Nevada			
	C. B. Spangler			
				Partial skull; "out of range."
				NYZ specimen (no acc. card); to AMNH 20 June 1888
				Collected prior to Sep 1903; died Aug 1905; skin to AMNH 5 Aug 1905
				Collected prior to 10 Apr 1928; died 6 Jul 1928; skin to AMNH (no record); gift of William J. Brunner
				Collected prior to 10 Apr 1928; died 8 Jul 1928; skin to AMNH (no record)
				Three specimens; no data, skins
				Received 1 Jun 1934; Urban J. Jones, Laureldale, Penn; died Jan 1939
				Received 1 June 1934, Urban J. Jones, Laureldale, Penn.; died Jan 1939
	F. J. Thompson			In alcohol; lost
			X	No data
			X	No data
			X	National Zoo specimen (no acc. card) to USNM
			X	National Zoo specimen (no acc. card) to USNM; skeleton only
				No data
				No data; probably belongs to skull in SCZ, Munich
				No data
	J. W. Munyon	Coues 1877		Platte River, not in current records
			X	"Out of range."

County) presented to the USNM sometime between 1872 and 1877 by Dr. V. F. Hayden. This specimen is no longer in the USNM collection. Hayden told Coues that another ferret was kept in captivity for some time at Greeley. Coues also examined the collection of the pioneer naturalist Mrs. M. A. Maxwell of Boulder and verified several specimens taken "in the vicinity of Denver" at a centennial exhibition in Washington, D.C., in 1876 (Coues 1877). The disposition of Mrs. Maxwell's collection is unknown. Both Hayden and Maxwell "represented the species as being not at all rare."

The most recent preserved specimen was obtained in Costilla County in 1946. Cahalane (1954) listed one specimen from Weld County in 1952, which was verified but subsequently
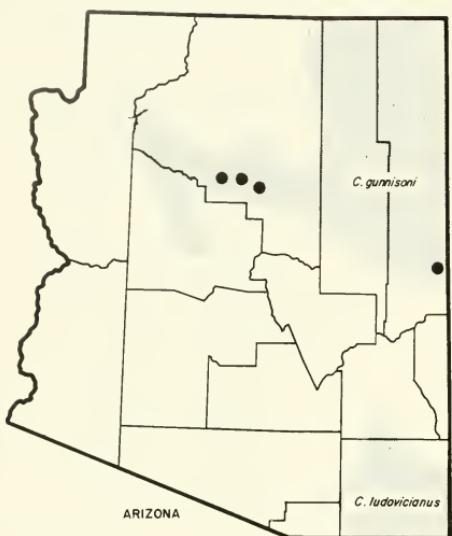
Fig. 10. Black-footed ferret specimens from Arizona. Prairie dog distribution (shaded) after Cockrum (1960).

destroyed. Eight of 10 of the most recent specimens (1940–1952) were collected west of the Front Range. One mandible was found in prairie dog colony searches in Logan County in 1977 (Bissell 1979), but, like many speci mens found ejected from burrows by prairie dog digging activity, it may have been under ground for an undetermined length of time before being brought to the surface. A record for Sedgewick County listed by Armstrong (1972) was found to be a sight record only and is not listed.

Two specimens were found above 2800 m. One of these (UCM 10658) was found in asso ciation with C. gunnisoni in Teller County at 2800 m. The other specimen (UCM 10660) was found drowned in Lake Moraine, eleva tion 3125 m in El Paso County, far from any prairie dog colony. This specimen and an other from Grand County (DMNH 653) were the only two specimens from Colorado not directly associated with prairie dogs and may have represented dispersing individuals.

Three species of prairie dogs occur in Colo rado: C. ludovicianus, C. leucurus, and C. gunnisoni. Burnett (1918) estimated that the three combined species occupied 5,665,720 ha in the state in 1918. The area now occupied by prairie dogs in the state is unknown, but it

is greatly reduced. Gilbert (1977) identified 10,843 ha of C. leucurus colonies in Rio Blanco and Moffat counties in 1977 and Bissell (1979) estimated 21,500 ha for 9 of 26 counties in C. ludovicianus range in the state in 1978. No estimate of C. gunnisoni distribution is available. Over 247,230 ha of C. gunnisoni- occupied colonies disappeared from 1945 to 1947 during epizootics of sylvatic plague (Armstrong 1972).

KANSAS

Occurrence of M. nigripes in Kansas was reviewed by Choate et al. (1982). We list eight additional records, including one specimen from Decatur County and one specimen in the CU collection dated 1883 (Table 6). Addi tional literature records include a mounted specimen from Wallace County examined by Coues (1877) supplied by L. H. Kerrick. About 1888 another ferret from Wallace County that had resided in the National Zo ological Park was given by Kerrick to the USNM (12299/22929). These are obviously different specimens, but whether Kerrick was associated with NZP or was the collector of the Wallace County animals is unknown. The dis position of several other animals residing at the NZP from 1905 to 1915 is also indicated in Table 6. Forty-eight specimens are known for the state (Fig. 12).

Of 18 ferrets in Table 6 collected from 1877 to 1890, 15 were collected by A. B. Baker. Several museum labels listing Baker as the collector also indicate the specimen was col lected under the auspices of the BSC, but it is not known whether Baker was employed by BSC. Recent specimens include one collected by hand in 1957 in Sheridan County (Taylor 1961) and a skull and mandible of unknown age found on a prairie dog town in Gove County in 1978 (Boggess et al. 1980).

Ferrets and prairie dogs historically occu pied most of Kansas west of the Flint Hills (Fig. 12). However, prairie dogs that occu pied an estimated 809,390 ha in Kansas in 1903 were reduced to some 14,570 ha (98% reduction) by 1973 (Choate et al. 1982). Choate et al. (1982) feel that ". . .the outlook is poor that the black-footed ferret will continue to occur in Kansas, if, indeed, any remain here now."
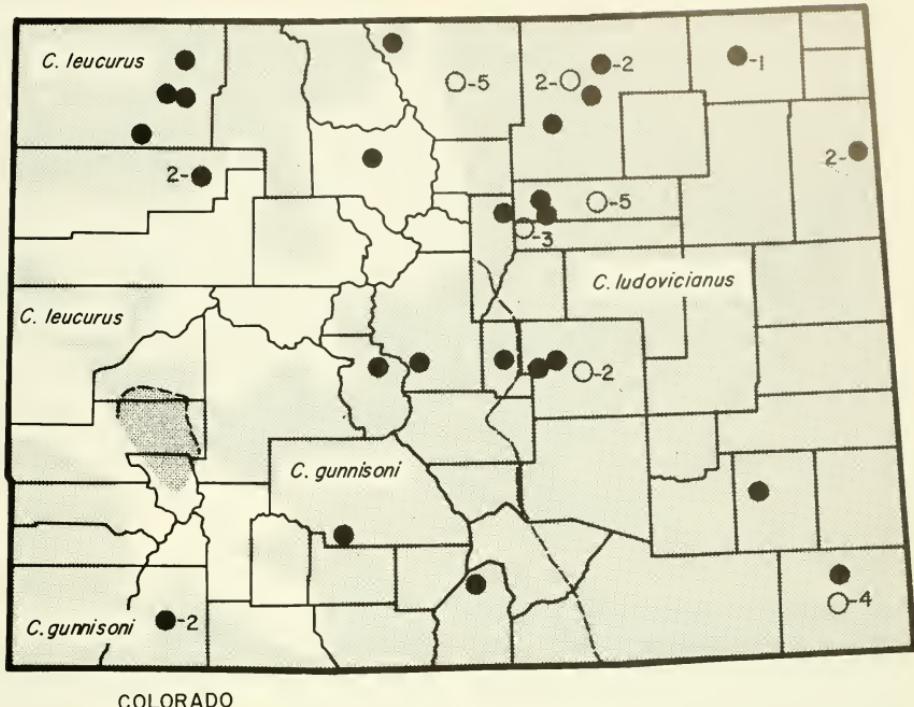
COLORADO

Fig. 11. Black-footed ferret specimens from Colorado. Prairie dog distribution (shaded) after Armstrong (1972).
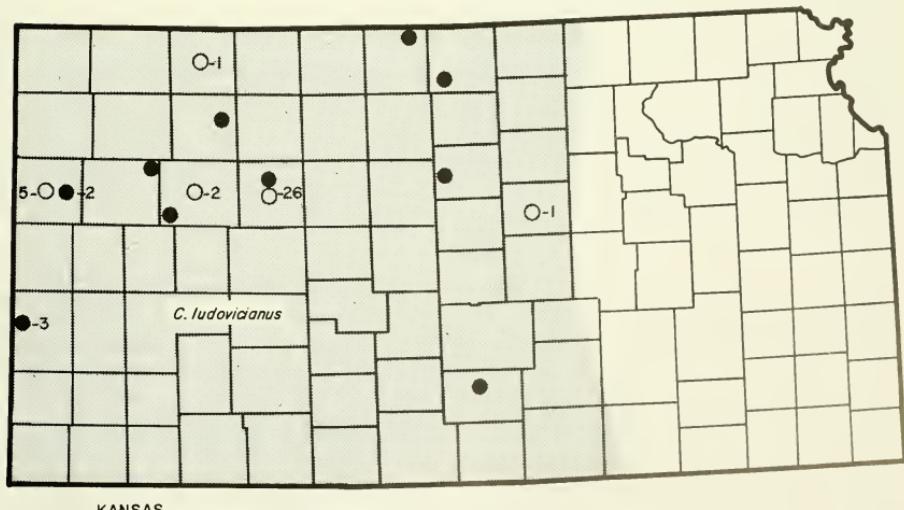
KANSAS

Fig. 12. Black-footed ferret specimens from Kansas. Prairie dog distribution (shaded) after Choate et al. (1982).
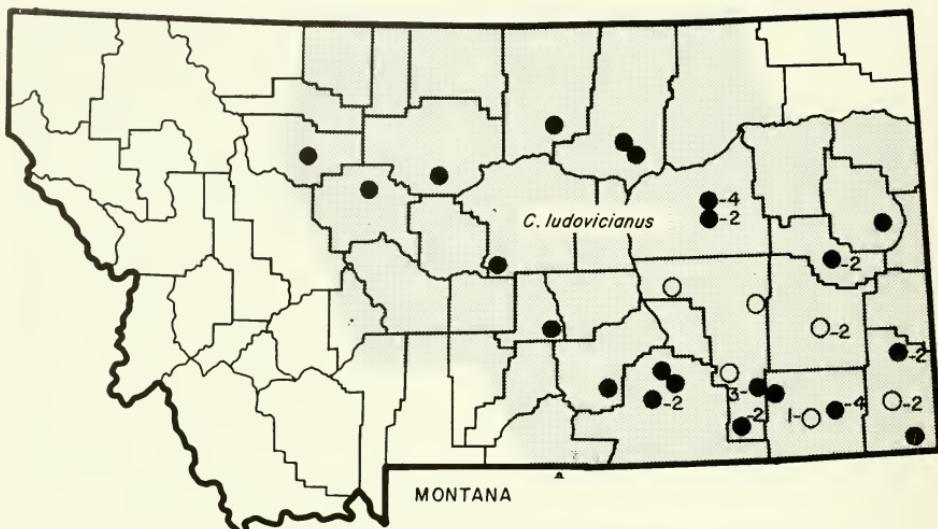
Fig. 13. Black-footed ferret specimens from Montana. Prairie dog distribution (shaded) after Hall (1981).

MONTANA

Specimens of the black-footed ferret from Montana have not been described. Forty-four specimens are known from the state (Table 6, Fig. 13). Coues (1877) reported the earliest specimen (now lost) from the "Milk River." The most recent specimen was taken in Carter County in 1953. Thirty two (73%) of these ferrets come from seven counties in the south-eastern part of the state. An undated specimen (USNM 13113/21976) lists the collection location near "Ft. Custer." Ft. Custer (in Bighorn County) was activated in 1877 and decommissioned in 1898, so it is assumed the specimen dates from that period.

Prairie dogs (*C. ludovicianus* except for a small intrusion of *C. leucurus* in southern Carbon County [Flath 1979]), occupy the eastern two-thirds of the state except the three extreme northeast counties (Daniels, Roosevelt, Sheridan) north of the Missouri River (Hall 1981). Historic distribution of prairie dogs in the Burlington Northern Rail-road right-of-way showed extensive contiguous areas (Flath and Clark 1986). Federal pro-grams poisoned 2,832,860 ha of prairie dog and ground squirrel habitat in Montana in 1920 alone (Bell 1921). Vigorous prairie dog control efforts continued on a statewide basis until the 1950s, and in some counties areas of

prairie dogs were reduced substantially (U.S. Bur. Land Mgmt. 1982). There is no estimate of the current total area occupied by prairie dogs in the state.

In 1984 and T. M. Campbell and SCF found two separate remains, a black-footed ferret skull and a mandible (MDFWP 2344a and 2344b) on a prairie dog colony in Carter County, where ferrets reportedly had been observed in 1977 (Jobman and Anderson 1981). From the condition of the remains and the recent occupancy history by prairie dogs in the area, it was estimated that they were no more than 10 years old, supporting the 1977 sighting. Repeated searches in the area failed to produce other evidence or observations of living animals.

NEBRASKA

Black-footed ferrets from Nebraska were recorded by Fichter and Jones (1953) and Jones (1964). We list an additional six speci-mens, for a total of 23 from the state (Table 6, Fig. 14). The most recent specimen was a road kill from Dawson County in 1949.

Additional information on two specimens is also available. A specimen mentioned by Coues (1877) and identified (USNM 14580) as coming from Nebraska has no date but should be about the time of the Coues report of 1877.
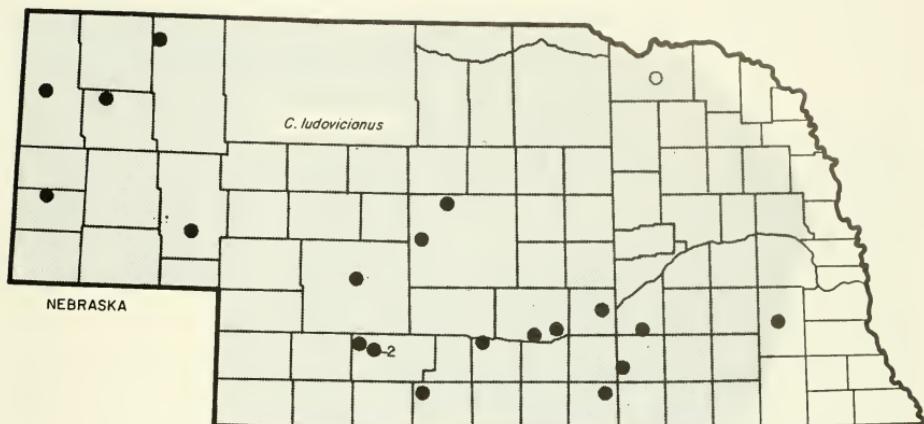
Fig. 14. Black-footed ferret specimens from Nebraska. Prairie dog distribution (shaded) after Jones (1964).

The whereabouts of a second specimen (Fichter and Jones 1953 #10) was unknown, but it is recorded correctly in Jones (1964) as AMNH 121610. We include all of the Fichter and Jones (1953) list except number 8, from Fremont, Dodge County, which was a secondary report.

Prairie dogs (*C. ludovicianus*) probably were restricted historically to the "hard lands" described in Fichter and Jones (1953), which excludes much of the north central Sand Hills region. No estimate of their historic abundance is available, but they probably were found in great numbers along the many tributaries of the Platte and Niobrara rivers. Lock (1973) estimated only 6070 ha of prairie dog colonies remained statewide in 1971.

NEW MEXICO

Status and history of the black-footed ferret in New Mexico are described in detail by Hubbard and Schmitt (1984). We include three records of "unsubstantiated" specimens in our list that are treated separately by them and described as "probable" or "highly probable." Because existence of these specimens is documented elsewhere, we include them here but concur with Hubbard and Schmitt (1984) that some question exists as to their validity. We also agree that a ferret mandible noted in Bailey (1926) as being found in Santa
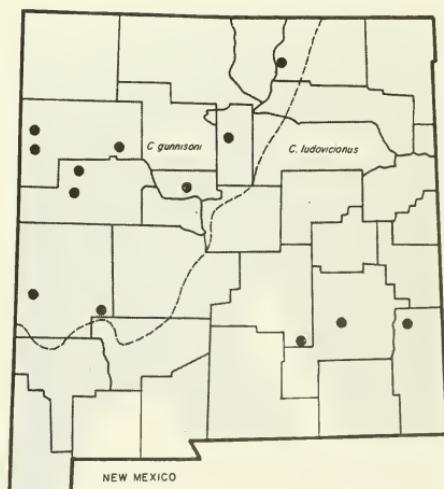
Fig. 15. Black-footed ferret specimens from New Mexico. Prairie dog distribution (shaded) after Hubbard and Schmitt (1984).

Rosa, Guadalupe County, in 1903 is the mandible catalogued in the USNM from Roswell, Chaves County, 1899 by Bailey.

We list 10 extant specimens and three disputed specimens (Table 6, Fig. 15). The last verified specimen was taken in 1934 in
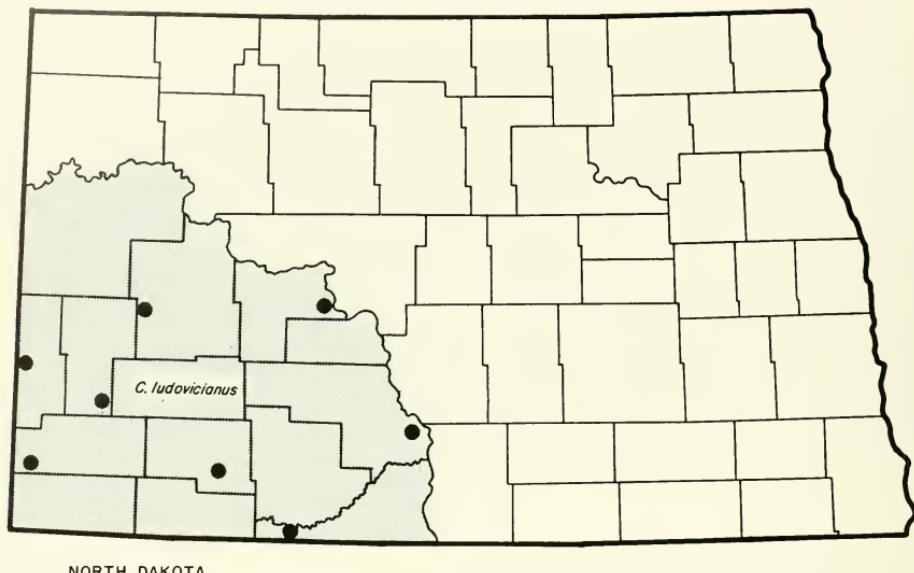
NORTH DAKOTA

Fig. 16. Black-footed ferret specimens from North Dakota. Prairie dog distribution (shaded) after Hall (1981).

McKinley County. Hubbard and Schmitt (1954) described the substantial role of BSC trappers in the collection of ferret specimens in the state.

Cynomys ludovicianus is found in the south- ern and eastern parts of the state, and *C. gunnisoni* is found at higher elevations in the northwest. Prairie dog area in the state de- clined from an estimated 4,856,333 ha in 1919 to less than 202,350 ha in 1979–1981 (Hub- bard and Schmitt 1984). Hubbard and Schmitt "assume the ferret is still a member of the state's fauna and that it could occur any- where that prairie dogs occur."

NORTH DAKOTA

No account of ferret specimens for North Dakota is available other than Bailey (1926). We located nine specimens, all collected west of the Missouri River (Table 6, Fig. 16). Re- cent specimens include one found in 1954 in Sioux County and a skull found in 1980 in southeastern Billings County.

Teddy Roosevelt described ferrets found near his ranch in western North Dakota in the late 1800s as "that rather rare weasel-like ani- mal . . . I have known one to fairly depopulate a prairie-dog town, it being the arch-foe of these little rodents" (Seton 1929: 571).

Little is known of former prairie dog (*C. ludovicianus*) distribution, although there were likely prairie dogs found east and north of the Missouri River. In 1920, 2,428,166 ha were treated with poisons for prairie dogs and ground squirrels in North Dakota (Bell 1921). Grondahl (1973) estimated only 2740 ha of prairie dogs remained by 1973, all west of the river. Seabloom et al. (1980:) ". . . regard sightings (of black-footed ferrets) as repre- senting transients rather than a viable resi- dent population" and cite the paucity of prairie dogs remaining in the southwestern part of the state.

OKLAHOMA

Lewis and Hassein (1973) listed recent fer- ret specimens and sightings for Oklahoma. Only four specimens are known, with one additional literature reference (Table 6, Fig. 17). A specimen was collected in Cleveland County in 1928, and Hibbard (1934) reported a ferret taken in Texas County in 1932. *Cyno- mys ludovicianus* probably occupied "mil- lions" of hectares in Oklahoma at the turn of the century, including one colony 35 km long in tall grass prairie between Kingfisher Creek and El Reno (Lewis and Hassein 1973), but only 3845 ha remained in 1968 (Tyler 1968).

Fig. 17. Black-footed ferret specimens from Oklahoma. Prairie dog distribution (shaded) after Hall (1981).

Black-footed ferrets were considered extir-pated in Oklahoma as of September 1980 by the U.S. Fish and Wildlife Service, Albu-querque, New Mexico (Jobman and Anderson 1981).

SOUTH DAKOTA

A detailed description of ferret distribution and occurrence is available for South Dakota, where ferrets were studied in Mellette and adjacent counties from 1964 to 1974. Hender-son et al. (1969) described ferret specimens and sight reports for South Dakota from 1889 to 1967, and additional records were dis-cussed in Linder et al. 1972. Table 6 includes an additional 15 specimens not in those ac-counts. Ninety-nine specimens are reported, with 57 specimens destroyed or of unknown disposition (Fig. 18).

Additional notes were also made for the fol-lowing specimens:

Moon (1905) noted a "pair sold alive" (Hen-derson et al. 1969: #6). The New York Zoolog-ical Park listed two arrivals of M. nigripes in October 1905, but no accession card was made to verify this transaction. A specimen that came from NYZP to AMNH (22894) on 1 June 1906 with no data was undoubtedly one of these animals. Disposition of the second ani-mal is unknown. We therefore list AMNH 22894 as coming from this source.

D. P. Stearns, BSC, captured one ferret alive near Pine Ridge, Shannon County, on 16 September 1923. This is undoubtedly the fer-ret trapped by BSC in Pine Ridge September 1923 reported by Linder et al. (1972). This animal was sent to the NZP (11281), where it lived until 4 November 1925. It was subse-quently catalogued into the USNM (243799).

Linder et al. (1972) listed 43 ferrets taken by BSC from 1924 to 1929. Table 6 lists 8 known specimens from that period. Four specimens in the SDMNH were taken in South Dakota during this period and correspond to the 3 specimens taken in 1928 not identified by month in the Linder et al. (1972) list and the 1 specimen from 1929. Therefore we have de-ducted them from the Linder et al. (1972) tally for those years. The remaining 4 specimens from that period may also have been collected by BSC, but insufficient data are available on the collectors to verify this. Both tallies are therefore included.

Rose (1973) briefly discussed the history of prairie dogs in South Dakota. Towns 24–32 km long were common in major drainages. H. R. Wells estimated 710,935 ha of prairie dogs in the state in 1923 (Linder et al. 1972). In 1968 BSFW estimated 24,281 ha in the state, a reduction of 96% (Rose 1973). Linder et al. (1972) presented data showing 405,000 ha were poisoned by various government agen-
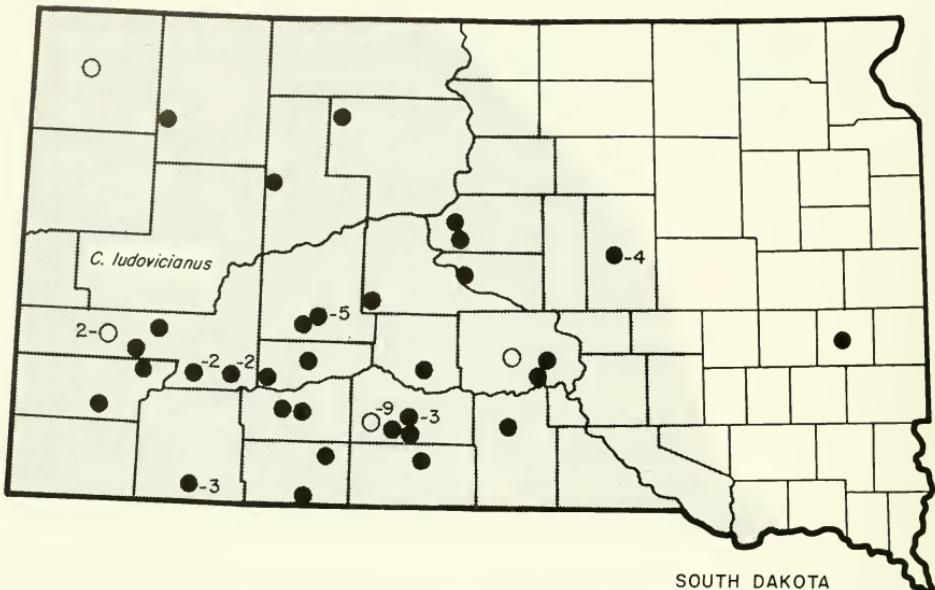
Fig. 18. Black-footed ferret specimens from South Dakota. Prairie dog distribution (shaded) after Hall (1981).

cies between 1932 and 1939. Three counties within the Pine Ridge Indian Reservation (Shannon, Jackson, Bennet) had recovered prairie dog populations occupying in excess of 120,000 ha in 1984 (R. Crete, personal communication).

TEXAS

The distribution of ferrets in Texas has not been described. We have established 13 verified records for the state and have located nine extant specimens (Table 6, Fig. 19). Specimen USNM 15018 is similar in all respects to a specimen described by True (1895) and is listed as such. Four specimens were taken for zoos. Two specimens from Gainesville are slightly out of current range, but may have been within historic range, or Gainesville may have been chosen by the collecter as the nearest identifiable landmark. The occurrence of ferrets in trans-Pecos Texas has been questioned (Schmidly 1977), even though it is highly likely they occurred there. None of these specimens expand the known range in the state.

Bailey (1905) estimated that prairie dogs (*C. ludovicianus*) occupied 233,100 sq km and
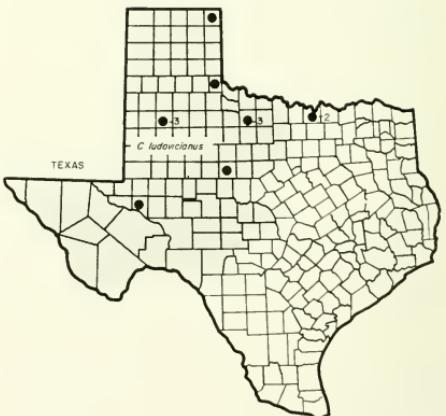
Fig. 19. Black-footed ferret specimens from Texas. Prairie dog distribution (shaded) after Cheatheam (1977).

noted one town in the Panhandle of 6,475,111 ha (400 x 160 km). A statewide survey in 1976 showed 36,432 ha of prairie dogs, which were nowhere in great density (Cheatheam 1977). The U.S. Fish and Wildlife Service, Albuquerque, New Mexico, considers the black-footed ferret extirpated in Texas (Jobman and Anderson 1981).

Fig. 20. Black-footed ferret specimens from Utah. Prairie dog distribution (shaded) after Durrant (1952).

UTAH

Only one specimen is known for Utah (Durrant 1952), found in 1937 south of Blanding, San Juan County (Table 6, Fig. 20). Three species of prairie dogs are found in Utah: *C. leucurus*, *C. gunnisoni*, and the endemic Utah prairie dog, *C. parvidens*. *Cynomys parvidens* is geographically disjunct and there is no evidence to suggest that *M. nigripes* has ever occurred with this species.

WYOMING

Black-footed ferret reports from Wyoming have been discussed in Clark (1980) and Clark and Campbell (1981), including an additional 126 sight records not listed here. In all, 60 ferret remains are known from 1851 to 1984, and 24 of these come from the Meeteetse area where the known population is currently under study (Table 6, Fig. 21). Five ferrets listed in Clark and Campbell (1981) were actually from South Dakota (Garst 1954). Ferrets
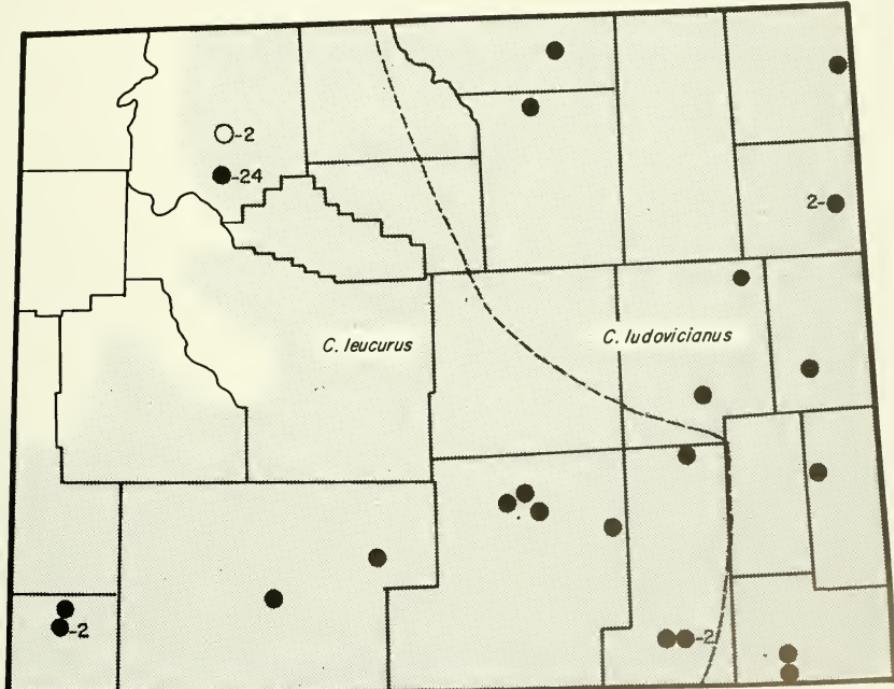
WYOMING

Fig. 21. Black-footed ferret specimens from Wyoming. Prairie dog distribution (shaded) after T. W. Clark, personal communication.
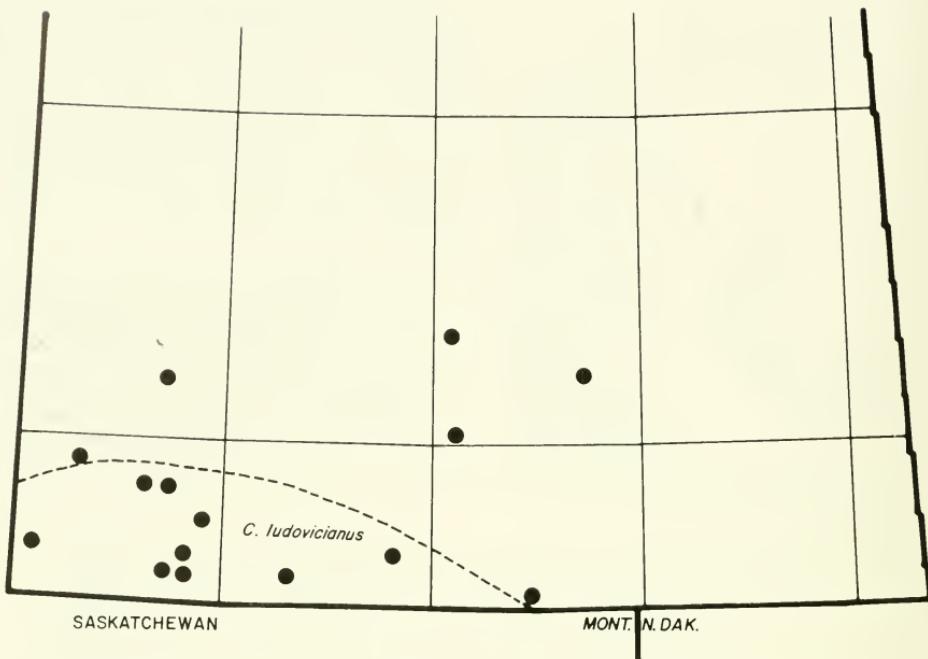
Fig. 22. Black-footed ferret specimens from Saskatchewan. Estimated extent of prairie dogs shown by dotted line.

range farther west in the state than previously reported by Hall (1981).

Ferrets occurred throughout Wyoming, except the mountainous northwestern corner, in association with *C. ludovicianus* in the east and *C. leucurus* in the west. Between 1915 and 1923, 1,120,290 ha were poisoned for prairie dogs (Martley 1954). An additional 445,080 ha were poisoned from 1923 to 1928 in Niobrara, Weston, and Campbell counties only, including one colony 160 km long from Indian Creek to Campbell County line (Day and Nelson 1929). Cheyenne, Wyoming, was built on the site of a large old colony (Day and Nelson 1929), where a ferret specimen was collected in 1877 (Coues 1877). Fragmentary records of prairie dog poisoning show that prairie dogs have been reduced by at least 75% since 1915 (Clark 1973). Clark et al. (1985) estimated that about 6,000 prairie dog colonies (ca 90,000 ha) still exist in Wyoming, but most are small and contain low densities of prairie dogs.

SASKATCHEWAN

Twenty-one specimens were located in one U.S. and four Canadian museums (Table 6). All of these specimens were collected in southern Saskatchewan with the exception of FMNH 8207, from Gleichen, Alberta (not mapped). Gleichen is several hundred kilometers out of present prairie dog range and is also disjunct from the next closest record of black-footed ferret in Saskatchewan. Because we have no other evidence to support ferret occurrence or recent prairie dog occurrence at that latitude at this time, we regard this record as spurious. It is possible the skin was picked up in fur shipments from another location and subsequently sold to FMNH.

Prairie dogs were not reported from Canada until 1927 (Soper 1938, 1944, 1946) and then only in the vicinity of Climax and Val Marie in extreme southwestern Saskatchewan. Ferret specimens were taken from 1924 to 1937 over a greater geographical area (Fig. 22). Prairie dogs may have been distributed at low densi-

ties or were expanding throughout southern Saskatchewan and Alberta at that time and were not recorded in biological surveys. Ground-dwelling rodents that might provide ferret habitat (with the exception of *Spermophilus richardsonii*) are absent in the area of ferret specimen distribution. Woodchuck (*Marmota monax*) and Franklin's ground squirrel (*S. franklinii*) are typically found at the eastern range of *Cynomys* in the continental U.S. and are found much farther north in Canada than the known distribution of prairie dogs (Hall 1981). Rather than imply an alternate habitat for the black-footed ferret in Canada, the distribution of ferret specimens more likely suggests the former range of *Cynomys*. The fossil history of *Cynomys* in Alberta goes back at least one million years. At Medicine Hat, *Cynomys* spp. has been found in Wisconsin-age deposits and *C. leucurus* has been identified in the Sangamonian and middle Wisconsinan faunas (Stalker et al. 1982). *Cynomys leucurus* has been at found at January Cave (late Wisconsin, J. Burns personal communication), and *C. ludovicianus* was recognized in the Hand Hills fauna (Storer 1975), although this identification has been questioned (J. Burns, personal communication). *Cynomys* has not been reported from any Pleistocene fauna in Saskatchewan. It is possible that intensive agriculture in the Prairie Provinces eliminated prairie dogs in many places before they could be recorded.

Prairie dogs totaled only 503 ha in 1971 and are currently found only near Val Marie (Kerwin and Scheelhaase 1971). Ferrets are considered extirpated in Canada by the Committee on the Status of Endangered Wildlife in Canada, 1978 (Thornback and Jenkins 1982).

ADDITIONAL REPORTS

Sixteen additional specimens are catalogued in museums with little or no identifying data (Table 6). Some of these may be the specimens that are "unknowns" from other locations. Some dates of acquisition can be guessed from catalogue numbers, but this is not reliable.

MCZ 14947, labeled as received in 1862, was collected by F. J. Thompson, who was the collector of record for Abilene, Taylor County, Texas, in 1882 (Coues 1882). This specimen was lost and may have been misla-

beled in the MCZ collection. Five of the specimens in this group were collected for zoos. Along with the Canadian evidence, additional reports outside the range of *Cynomys* are specimen USNM 21965 listed from Licks River, Missouri, and a note by Ames (1874) listing "*P. nigripes*", with no evidence, in the fauna of Minnesota. However, these reports are far from potential range as determined by prairie dog distribution, and we conclude they are erroneously placed as originating in these locations. In the case of the Missouri account, for example, the specimen could have been taken on the Kansas plains and subsequently ascribed by the collector to his home location. No place name for Lick's River in Missouri could be found.

Summary

We list 412 specimens in Table 6. The current deposition is known for 310 of them. The largest number of state records (99) and extant specimens (50) are from South Dakota. Twenty-one specimens are noted from Canada. Only 6 specimens were collected outside of known prairie dog range, although the association of some of the Canadian specimens is uncertain. Of the 412 records, at least 103 (25%) were taken by federal predator and rodent control agents. The number taken by museum collectors is unknown but probably is also significant. At least 41 animals (10%) were captured alive and held by individuals or zoos.

Specimens collected by year are given in Figure 23 (n = 318). The highest collection figures date from the 1920s. This peak corresponds to the period in which the BSFW was entering numerous agreements with state extension services in the West to control prairie dogs and carrying out large-scale poisoning campaigns (Day and Nelson 1929, Linder et al. 1972, Hubbard and Schmitt 1984). Because ferrets never have been of economic value, many specimens that were taken up to this time probably were destroyed and never reported. Elsewhere, changing land use significantly reduced potential ferret habitat and contributed to ferret decline. In several eastern prairie states (Kansas, Nebraska, Oklahoma, Texas), 65% of all specimens collected date prior to 1910. The early demise of ferrets in these states is probably directly attrib-
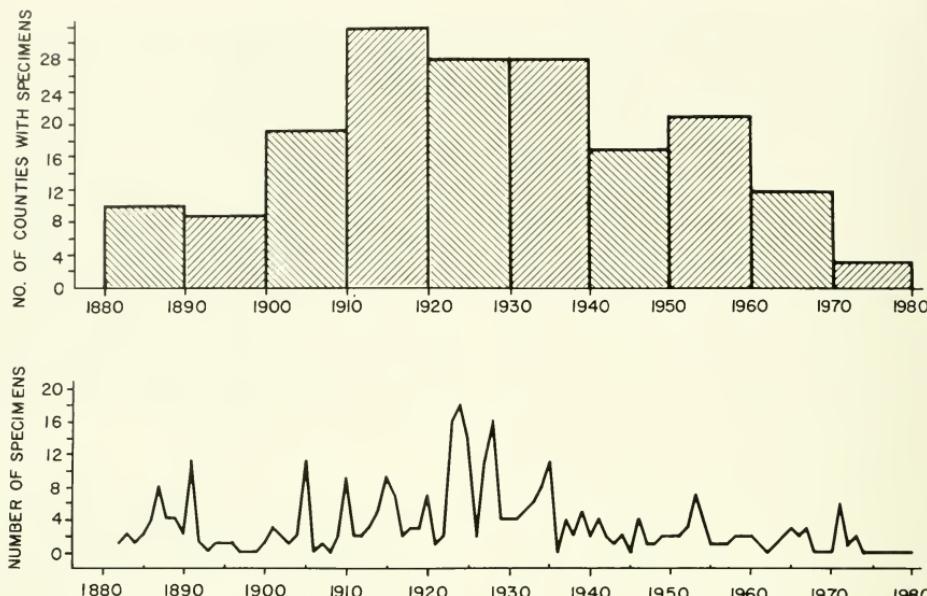
Fig. 23. Collection history of black-footed ferret specimens by county and by year (1880–1980).

utable to the expansion of population and culti vation into areas formerly occupied by prairie dogs.

In the 1950s disappearance of large areas occu pied by prairie dogs stimulated interest in locat ing all possible remaining ferrets, but despite the more detailed accounting of sight and speci men reports (e.g., Cahalane 1954), specimen re ports continued to decline, including the num ber of counties reporting specimens (Fig. 17). By the 1970s the number of known populations had dwindled to one, although in retrospect the pop ulation at Meeteetse was certainly extant as well as some individuals in Carter County, Montana. At the present time only the Meeteetse popula tion is known.

Plotting locality records of ferrets with the ranges of three species of prairie dogs shows 83.0% are from *C. ludovicianus* range, 11.2% are from *C. leucurus* range, and 5.8% are from *C. gunnisoni* range. Our estimates of prairie dog abundance show that 41,900,000 ha of rangeland may have been occupied by all species of prairie dogs in the early part of the 1900s. Nelson (1919) estimated 40,469,500 ha. Current areas occu pied in all the western states and provinces is unknown but is greatly reduced, perhaps by as

much as 90%. Presently, ferrets are consid ered extirpated by U.S. and Canadian wildlife officials in Canada, Oklahoma, and Texas. Be cause of low prairie dog numbers, the likeli hood of persistence of black-footed ferrets in Arizona, Kansas, Nebraska, and North Da kota is also poor. Ferrets may persist in the remaining states of its former range, but they are probably restricted to small, isolated pop ulations.

Specimen collection by month is plotted in Figure 24. Seasonal changes in collection re turns likely reflect phases in ferret life history and trapping efforts. Since trapping for most furbearers reaches its peak in midwinter, high returns are to be expected, particularly where ferrets are caught accidentally in sets for other animals. It is interesting to note that the peak month of collection is October, the time at which most newly independent young ferrets are dis persing (D. E. Biggins, personal communication cited in Forrest et al., *Black-footed ferret habi tat*, 1985). The lowest specimen count occurs in June, when females with young remain for long periods underground.

Several authors have commented on the bias toward males in capture data for mus-
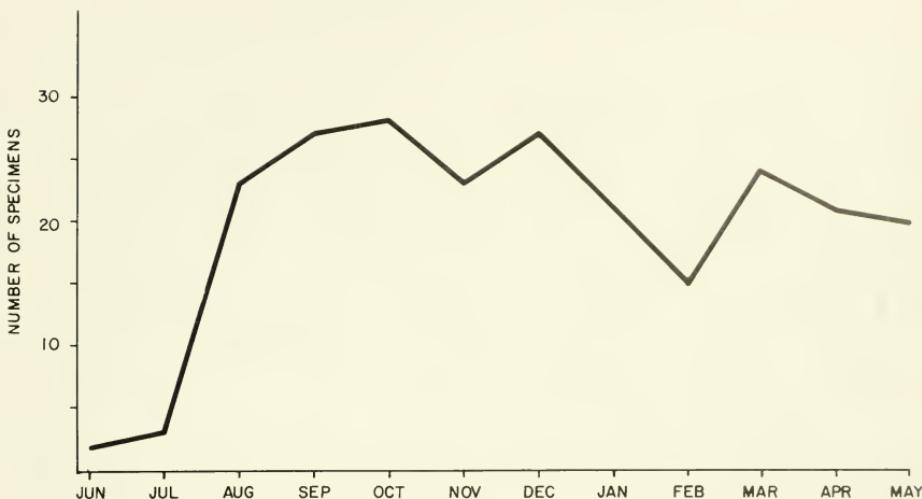
Fig. 24. Collection of black-footed ferret specimens (n = 234) by month based on all records (1851–1984).

telids (King 1975). The 200 ferret specimens of known sex in Table 3 (137 males and 67 females) show a sex ratio of 2.04M:1F. Since sex ratios at birth are 1:1 (Forrest et al., *Life history characteristics*, 1985), it seems likely that this collection bias is similar to trap biases seen for other mustelids, and is not a result of a skewed adult sex ratio. Trap biases in mustelids are a result of males having larger activity areas and longer movements (and therefore more encounters with traps or hazards) and being less trap-shy (King 1975, Powell 1979). Black-footed ferret males have larger activity areas (Biggins et al. 1985, Richardson et al. in preparation), which further supports this theory.

MORPHOMETRIC VARIATION

Sexual Dimorphism

Adult females averaged 93% of male body length for both museum- and field-measured groups and were 68% of males in body weight. Skull length for females averages 93% of that of males based on CBL.

Five variables were chosen by stepwise maximizing of Wilks' lambda for cranial measurements as the best discriminators of sex: CBL, LC, POC, INB, and WM^1. The results of the cranial discriminant analysis produced excellent discrimination between classes (Fig. 25). Coefficients for known specimens not
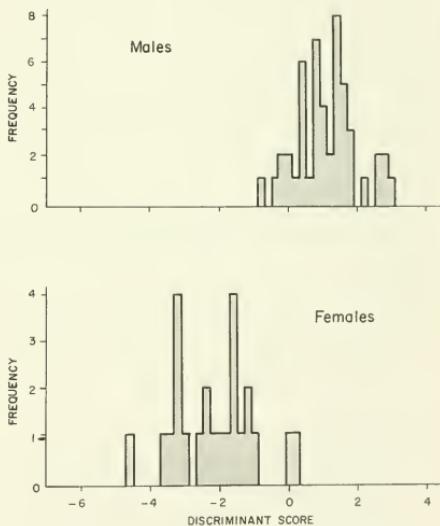
Fig. 25. Histogram of discriminant scores from a discriminant analysis between sexes of black-footed ferrets.

used in classification indicated that only 2.0% of males and 8.3% of females were misidentified on this basis, or that grouped cases were correctly classified 95.9% of the time. Because in many cases only mandibles may be found (particularly with fossil material), a second analysis using only mandibular variables
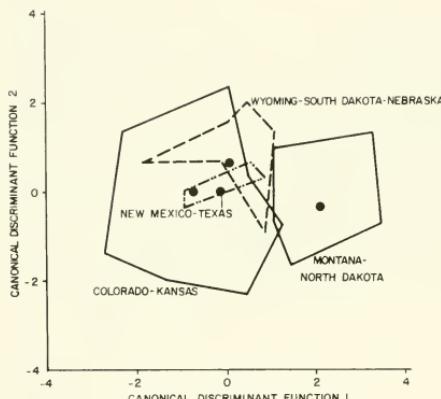
Fig. 26. Convex polygons containing the values for specimens of male *M. nigripes* from four localities (north-south) for their first two discriminant axes.

Fig. 27. Convex polygons containing the values for specimens of female *M. nigripes* from four localities (north-south) for their first two discriminant axes.

was made. Four mandibular variables (LJAW, DP_{3-4}, WM_1tal, and LM_1tr) were chosen by maximization of Wilks' lambda. Mandible measures are not as good as cranial measures as discriminators of sex, with 8.2% of males and 16.7% of females correctly classified (correct classification 89.4% of the time), but they can be used when crania are not available or cannot be classified.

To assign sex to crania and mandibles a decision is made based on the following equations derived from the discriminant analysis. For crania:

$A = 19.954(CBL) + 14.129(INB) + 0.373(LC) + 24.790 (POC) - 29.706(WM^1) - 877.213.$

$B = 18.936(CBL) + 11.681(INB) - 5.634(LC) + 23.099 (POC) - 23.600(WM^1) - 758.034.$

For mandibles:

$A = 10.279(LJAW) + 13.849(DP_{3-4}) + 93.278(WM_1tal) + 65.965(LM_1tr) - 591.915.$

$B = 9.435(LJAW) + 11.416(DP_{3-4}) + 85.110(WM_1tal) + 63.392(LM_1tr) - 502.990.$

If $A > B$, then the skull is from a male. If $B > A$, then the skull is from a female. If the absolute difference between A and B is greater than 2.80, then $P > .05$ that the skull has been correctly classified. If $A = B$ or the difference between A and B is less than 0.50, then the probability of correct classification is less than 60%, and no determination can be made as to sex.

Geographic Variation

Linear discriminant analysis was performed on 29 cranial measurements of 50 males and 31 females from four geographic regions that correspond roughly to four latitudinal gradients arranged from north to south (Fig. 1). These regions were: Montana–North Dakota; Wyoming–South Dakota–Nebraska; Colorado–Kansas; New Mexico–Texas–Arizona.

The characters best separating males by region were: CBL, DP_{3-4}, LP^4, WM^1, and PBC-C. Characters best separating females by region were: CBL, DP_{3-4}, LP^4, WM^1, PBC-C, and WP^4pc. Discriminant scores and group centroids for the first two discriminant axes are shown in Figure 26 (males) and Figure 27 (females). There is evidence in this analysis of a north-south cline for both sexes, although overlap between clinal groups can be seen (Table 7). The extreme southern region (New Mexico-Arizona-Texas), overlaps the Colorado-Kansas region for males and appears separated on the axis for canonical function 2 for females. The southern group is included for completeness despite the obvious violation of multivariate assumptions caused by extremely small sample sizes. The present orientation of centroids is little affected by this region because of these small sample sizes. This partially explains high misclassification for both males and females in this group. Outcomes of discriminant classification in Table 7

TABLE 7. Discriminant classification of male and female black-footed ferrets from four localities showing number of members from each location correctly classified.

Actual group	Number of cases	Predicted group membership			
		1	2	3	4
FEMALES: 72.73% of "grouped" cases correctly classified					
1 (Montana, North Dakota)	8	6 (75.0%)	2 (25.0%)	0	0
2 (Wyoming, South Dakota, Nebraska)	7	1 (14.3%)	5 (71.4%)	1 (14.3%)	0
3 (Colorado, Kansas)	16	3 (18.8%)	0	11 (68.8%)	2 (12.5%)
4 (New Mexico, Arizona, Texas)	2	0	0	0	2 (100.0%)
MALES: 56.86% of "grouped" cases correctly classified					
1 (Montana, North Dakota)	8	7 (87.5%)	1 (12.5%)	0	0
2 (Wyoming, South Dakota)	8	1 (12.5%)	4 (50.0%)	1 (12.5%)	2 (25.0%)
3 (Colorado, Kansas)	31	2 (6.5%)	5 (16.1%)	17 (54.8%)	7 (22.6%)
4 (New Mexico, Arizona, Texas)	4	0	2 (50.0%)	1 (25.0%)	1 (25.0%)

show higher overlap of nearer clinal groups and little or no overlap as clinal groups become farther apart.

Further analysis reveals that the source of this variation is primarily found in differences in size from north to south and not in changes in relationships of variables to each other. This is indicated by Figure 28 for CBL, which shows significantly larger measurements between northern and southern groups for both males and females (males: $F = 4.3$, 44 df, $P = .04$; females: $F = 5.1$, 25 df, $P = .03$). ANOVA between the two northernmost and two southernmost groups showed significant differences in 17 of the 29 variables tested, with larger measurements from the northern group.

Prey Species Variation

Discriminant analysis was also used to test for differences between ferret specimens associated with different prairie dog species. The subgenus *Leucocrossuromys* includes *C. gunnisoni*, *C. leucurus*, and *C. parvidens*. The subgenus *Cynomys* includes *C. ludovicianus* and *C. mexicanus* (Mexican prairie dog). *Leucocrossuromys* is considered more like ancestral *Spermophilus* than *Cynomys*; shows a less interactive social organization, organized around clans; and has a short white-tipped tail, a less massive skull, and smaller and less expanded cheek teeth (Clark 1973a). Subgenus *Cynomys* has a longer black-tipped tail, distinct reddish-cinnamon pelage in summer, and a more complex social organization than *Leucocrossuromys*, organized around
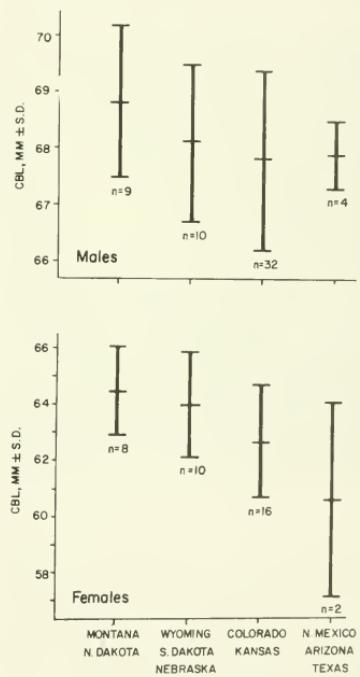
Fig. 28. Latitudinal differences in CBL for male and female black-footed ferrets showing a north-south cline in size.

coteries (King 1955, Hoogland 1981). The current distributions of the two subgenera show an elevational and longitudinal cline, since the white-tailed species is found at higher elevations along the western portion of prairie dog range. Since the subgenera occur at dif-
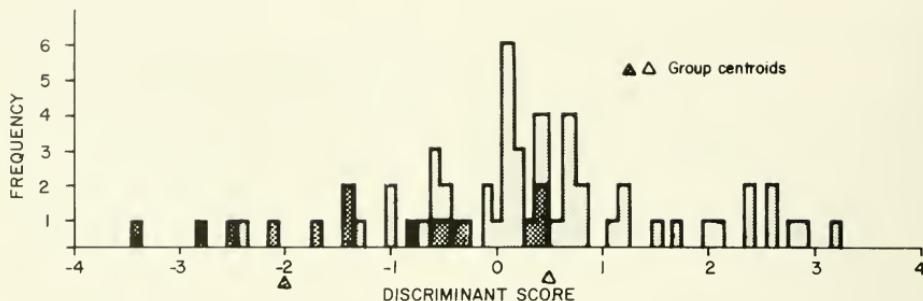
Fig. 29. Histogram of discriminant scores from a discriminant analysis between *M. nigripes* specimens taken from black-tailed prairie dog range (dark shading) and white-tailed prairie dog range (light shading).
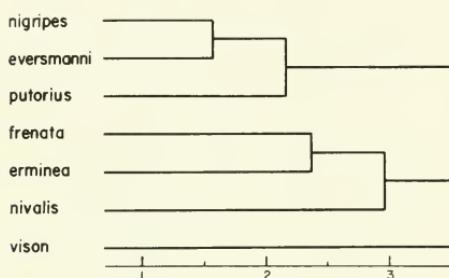
Fig. 30. Single linkage dendrogram using generalized distances between species centroids based on a consensus of *Mustela* males and females (after Youngman 1982).

ferent densities, have different behavior pat terns, and are geographically separated, it might be expected that ferret differentiation may have evolved with each subgenus of prairie dog, which could be reflected in mor phological differences. For example, prairie dogs show similar external sizes and dimen sions among species (Hall 1981) but may differ along similar latitudinal gradients. Size differ ences could be reflected in the size of burrow openings used and weight of the animal, which could in turn affect the size or confor mation of ferrets found with them.

Because of north-south clinal variation and sexual variation among ferrets, comparisons were made only between male ferrets from the range of black-tailed prairie dog (n=50) and ferrets from the range of white-tailed prairie dog (n=15) subgenera from the two regions closest to the geographic center of ferret range (Wyoming-South Dakota-Ne braska and Colorado-Kansas). Although six

variables (1NB, WBC, WM_1tr, $LC-M^1$, WC, and WM_1tal) were chosen by stepwise maxi mizing of Wilk's lambda, which discriminated between white-tailed and black-tailed prey groups, only 53.3% of the white-tailed group were placed correctly in that category, indi cating a high degree of overlap between groups (Fig. 29). This analysis suggests that no morphometric variation in black-footed fer rets occurs based on the species of prairie dog they are found to associate with. However, other differences may exist that involve eco logical or behavioral characteristics that could taxonomically separate these groups but are not reflected in morphometric analyses.

Ferrets and Their Relatives

The genus *Mustela* includes weasels (sub genus *Mustela*), mink (subgenera *Lutreola* and *Vison*, see Youngman 1982), ferrets and polecats, (subgenus *Putorius*; European workers often use *Putorius* as a generic name), and South American weasels (subgenus *Grammogale*). "Ferret" and "polecat" are interchangeable common names, though polecat is generally used for the Old World species. Based on single linkage dendrograms derived from morphometric variables, Youngman (1982) suggested that the polecats *M. putorius*, *M. eversmanni*, and *M. ni gripes*, form a natural group distinct from the weasels and *M. vison*. Figure 30 shows the phylogenetic relationships of some of the spe cies in this group. These highly efficient small carnivores range in size from the tiny least weasel (*M. nivalis rixosa*, wt 38–63 gm), the smallest living carnivore, to the Siberian or steppe polecat (*M. eversmanni*, wt to 2050

Fig. 31. Photographs of *M. nigripes* (A), *M. vison* (B), *M. eversmanni* (C), and *M. putorius furo* (D).

gm). All of them have a long lithe body, short legs, a long low braincase, and short powerful jaws equipped with elongated bladelike car- nassials (P^4, M_1), sharp canines, and three premolars in each jaw half (two in the lower jaw of the South American weasel, *M. africana*). Primarily Holarctic in distribution, weasels and ferrets are terrestrial and mink semiaquatic. About 15 extant species are rec- ognized.

Of these, only four, *M. nigripes*, *M. evers- manni*, *M. putorius*, and *M. vison*, concern us here. Table 8 compares the four species and Figure 31 illustrates them. Although mink and ferrets differ markedly from each other in appearance, their skulls and teeth are similar and can be confused. Table 9 shows some differences between them.

The domestic ferret (*M. putorius furo*) was bred in captivity as early as the fourth century B.C. for use in controlling rodents and driving rabbits from their burrows (Nowak and Par- adiso 1983). It is also kept as a pet. Leonardo da Vinci's famous painting "The Lady with a Weasel" actually depicts the domestic fer- ret (Kowalski 1976). Its distribution is now worldwide in captivity. Coloration is gener- ally pale yellow or whitish (often albino) with no black or dark markings. Escaped domestic ferrets have been mistaken for black-footed

TABLE 8. Comparisons between *Mustela nigripes*, *M. eversmanni*, *M. putorius*, and *M. vison*.

	M. nigripes	*M. eversmanni*	*M. putorius*	*M. vison*
Geologic range	Early late Pleistocene–Recent	Mid-Pleistocene– Recent	Mid-Pleistocene– Recent	Mid-Pleistocene– Recent
Geographic range	Formerly S Canada, Great Plains to NW Texas, SW U.S.	Steppes of Eurasia, S to central Asia, NE China	Europe E to Ural Mountains	North America except arid areas. Introduced in Europe
Habitat	Prairies, mountain basins, semiarid grasslands	Open grasslands	Open forests, meadows, clearings	Along streams, marshes
External characters	Upper parts yellowish buff. Feet black, black mask across eyes, tail tip black	Yellowish to pale brown. Dark feet, dark mask across eyes, terminal 1/3 tail dark	Dark brown to black, belly dark, silvery between eyes and ears, tail entirely dark	Rich dark brown, white chin patch, tail slightly bushy
Size	♂ TL 490–615, T 107–148, Wt 915– 1125 g. ♀ TL 479– 565, T 109–141, Wt 645–850 g.	♂ TL 450–740, T 80–183, Wt to 2050 g. ♀ TL 360–700, T 70– 180, Wt to 1350 g.	♂ TL 465–650, T 115–190, Wt 500– 1500 g. ♀ TL 375– 465, T 85–125, Wt to 1360 g.	♂ TL 510–570, T 180– 230, Wt 680–1360 g. ♀ TL 430–560, T 130– 200, Wt 565–1089 g.
Food	*Cynomys*, rodents, lagomorphs	Pikas, susliks, voles, hamsters, marmots	Mice, toads and frogs, birds	Aquatic mammals, birds, frogs, fish, crayfish
Habits	Mostly nocturnal, solitary. Closely associated with *Cynomys*	Nocturnal. Live in rodent burrows. Avoids contacts with man	Nocturnal, solitary. Often found around barns, dwellings	Nocturnal, solitary. Den along streams
Reproduction	Gestation period 42– 45 days. 3–5 young born May–June	Gestation period 38– 41 days. 4–9 young born April–May	Gestation period 40– 43 days. 4–6 young born May–June	Gestation period 40–91 days. Short delayed implantation. 2–6 young born April–May
Remarks	Endangered species. Closely related to *M. eversmanni*.	Striking resemblance to *M. nigripes*. Hunting of *M. e.* prohibited in Siberia	Fur valuable (fitch). Subspecies *M.p. furo* domesticated, used in hunting and as pets	Fur valuable. Raised on fur farms

TABLE 9. Comparisons between *Mustela nigripes/eversmanni* and *M. vison* (after Anderson 1977).

Variant	*M. nigripes/eversmanni*	*M. vison*
Palate	Wide between canines	Narrow between canines
Basiocciput	Narrow	Wide
Basicranium	Well-developed tube extending from foramen ovale to anterior margin of auditory bulla	No tube. Area between foramen ovale and auditory bulla flat
Auditory bullae	More inflated	Less inflated
Auditory meatus	External opening large	External opening small
Mastoid bullae	Inflated	Not inflated
Infraorbital foramen	Small	Large
Jugal	Wide	Narrow
Frontals	Rounded	Flattened
Canines, upper and lower	Relatively large	Relatively small
P^3	Short, broad	Long, narrow
P^4	Relatively short protocone	Relatively long protocone
M^1	Inner lobe not expanded	Inner lobe expanded
Mandible	Relatively short and thick	Relatively long and slender
Inferior margin of jaw at angle	Broad, flattened	Narrower, less flattened
Lower premolars	Relatively short, broad	Relatively long, slender
M_1	Metaconid absent, talonid narrow	Incipient metaconid, talonid broad
M_2	Relatively small	Relatively large

ferrets (Choate et al. 1982), but they are entirely different in appearance (Fig. 31).

Polecats probably arose in Europe in the Villafranchian (3–4 mil yrs B.P.). The earliest known species, Stromers polecat (*M. stromeri*), ranged from the late Villafranchian to the middle Pleistocene, when it was replaced by the modern species. Though smaller in size, Stromer's polecat was closely allied to the European polecat (*M. putorius*) and was probably ancestral to both the European polecat and the steppe polecat (*M. eversmanni*). These two polecats have been considered conspecific by some workers, but studies by Russian mammalogists (Stroganov 1962) have shown them to be distinct, well-defined species that differ in size, coloration, and habitat. Although their ranges overlap in Hungary, Romania, and southern European Russia, they are nowhere truly sympatric, being separated by different habitat preferences (Corbet 1966). Hybrids occur only under exceptional circumstances. Unlike *M. nigripes*, the steppe polecat is not closely associated with any one species of rodent and feeds on susliks (*Spermophilus* spp.), marmots, hamsters and voles; in winter, pikas (*Ochotona* spp.) are a major food source in some areas. Rodent burrows, especially those of susliks, are often expropriated by polecats for shelter and dens, though they may dig their own. *Mustela eversmanni* is valued as an exterminator of rodents and for its fur, which is, however, of lower quality than that of *M. putorius*. Although *M. eversmanni* is not considered to be endangered, hunting the animal in Siberia is prohibited.

Mustela eversmanni and *M. nigripes* are closely related, and their possible conspecificity has been noted by several workers (see Youngman 1982 for references). Although their size and coloration are similar, and analysis shows only slight differences in cranial and dental measurements (Figs. 20, 21, 22), Anderson (1977) considers them separate entities.

That the two species are closely related cannot be doubted, but until detailed comparative and statistical studies are made on the large collections of *Mustela eversmanni* in Soviet institutions, these data are compared with the information already compiled on *Mustela nigripes*, and behavioral and chromosomal studies are undertaken on both species, I regard them as distinct.

Detailed studies are still lacking for *M. eversmanni*, and so far there have not been any studies on genetic variation between the two species, so the question of *M. eversmanni* and *M. nigripes* conspecificity remains unresolved.

Another taxonomic problem in the ferrets is the recognition of subspecies. No subspecies of *M. nigripes* have ever been named, and our studies do not show any taxonomically significant geographic variations between samples. Two or perhaps three subspecies of *M. putorius* are recognized based on slight differences in size and color. Seventeen subspecies of *M. eversmanni* have been described, eight of them from Siberia. Strogonov (1962:370) said, "The Siberian polecat shows more geographical variation than the European polecat, this being manifested in changes in fur structure and in dimensions of body, skull and claws." Whether all of these subspecies are valid or merely represent oversplitting is unknown. Of the three species of polecats, *M. eversmanni* has by far the largest geographic range, extending from Hungary to far eastern Asia across the broad band of steppes, forest steppes, and semideserts between 50° and 60° N latitude.

The historic range of *M. nigripes* included the Great Plains and mountain valleys. This was a relatively homogeneous environment without major geographic barriers. However, Endler (1977) points out that there is no evidence that allopatry is necessary for differentiation. Gradation within a continuous range (parapatry) is very common, as is pointed out by the north-south differentiation demonstrated for *M. nigripes* in this paper. Additional specimens from the northern and southern extremes of the range would probably demonstrate more strongly this clinal variation. Whether geographic isolation, for example, in South Park, Colorado (USNM 247073), would eventually have resulted in distinct subspecies will, of course, never be known.

Ferrets entered North America from Siberia, spread across Beringia, and then advanced southward through icefree corridors to the Great Plains. Kalela (cited in Kurtén 1957) noted that between 1880 and 1940, *M. putorius* extended its range in Finland from the Karelian Isthmus north to central Os-

trobothnia and west to the Gulf of Bothnia at a rate of 7.5 km annually or 750 km/century. This rate is probably applicable for ferrets spreading across Siberia into the New World in the Pleistocene, when conditions were favorable.

DISCUSSION

Our evidence supports the contention of others (e.g., Linder et al. 1972, Hubbard and Schmitt 1984) that black-footed ferrets were probably common historically. We have lo cated physical remains or verified reports of ferrets from 128 of 513 counties (25%) within the historic range of *Cynomys*. A conservative estimate is that 41,000,000 ha of western grasslands were occupied by prairie dogs in the early part of this century. Using the For rest et al. (*Life history characteristics*, 1985) population density estimate of one ferret per 40–60 ha, habitat may have been available in the past to support as many as 500,000– 1,000,000 black-footed ferrets, if this habitat were fully occupied by ferrets.

Although the Canadian specimens cast some doubt on the nearly obligate association between ferrets and prairie dogs, it is almost certain that alternate habitats do not provide adequate resources to support ferrets in the long term. If ferrets were living in habitats other than prairie dog colonies in Canada, then they should still be extant there; yet the last specimen was taken in 1937, about the time remnant prairie dogs in Canada were being eliminated by expansion of agriculture.

Geographic variation in a species has implications for any recovery program involving reintroduction of animals into areas where they have been extirpated. It would not be prudent to attempt such reintroductions us ing animals that differ greatly from those that originally occurred in the reintroduction area. However, with black-footed ferrets there seems to be little habitat-related variation, and reintroductions should prove successful in any geographic area with any prairie dog species serving as prey, provided sufficient habitat still remains to support the ferrets and their prey. With regard to clinal or other geographic variation, our analyses suggest that a case can be made for morphometric variation within this species, although the usefulness of this argument seems limited to the case where numerous populations are competing for pro-

tection (Schonewald-Cox et al. 1985), which is not the case for this species.

The possibility that the steppe ferret and the black-footed ferret are representatives of a single holarctic species exploiting similar eco logical niches in the New World and Old has been suggested. This in no way diminishes the unique position the black-footed ferret holds in the prairie ecosystems of this conti nent. It does suggest that options that might draw on *M. eversmanni* to assist in recovery efforts for the endangered *M. nigripes* should be further explored.

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HISTORIC STATUS OF BLACK-FOOTED FERRET HABITAT IN MONTANA

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ABSTRACT.—Black-footed ferrets (*Mustela nigripes*) use prairie dogs (*Cynomys* spp.) for food and their burrows for shelter. Thus, prairie dog colonies are essential ferret habitat. Prairie dog control, which resulted in permanent loss of ferret habitat, is considered the primary reason for the ferret's endangered status today. Northern Pacific Railroad (presently Burlington Northern) lands were surveyed 1908–1914, just prior to the onset of widespread prairie dog control. In Montana the surveyed area included a belt about 483 km long and 192 km wide, from the Montana-North Dakota border westward to Livingston. In all, 6,661 sections (11.8%) of 22 counties were surveyed and 1,662 of these sections (24.9%) contained at least some prairie dogs. Prairie dog colonies (N = 1,985) occupied all or part of 5,186, 16 ha (40ac) parcels and totaled a minimum of 47,568 ha, with a mean colony size of 24.5 ha (2.8% of the landscape in colonies). Two township-wide belt transect samples—T4N and R45E—showed colonies were clumped in distribution. Two areas with large complexes of colonies are illustrated, and each area exceeded an estimated 15,000+ ha. The Tongue River-Otter Creek area had at least 20 complexes, with a mean intercomplex distance of 3.4 km; and the Powder River-O'Fallon Creek area had at least 33 complexes, with a mean intercomplex distance of 2.9 km. Historic land uses were similar to today's uses—grazing and a few crops. Historic prairie dog areas in Montana occupied an estimated 5,953 sq km. An estimated 90+% reduction in prairie dogs has occurred since 1914, largely if not totally due to poisoning. The elimination, fragmentation, and greatly reduced size of ferret habitat has undoubtedly contributed to the endangered status of ferrets. A few areas in Montana appear to contain enough prairie dogs to potentially harbor ferret populations. These areas could serve as reintroduction sites for ferrets, as well as examples of complex prairie dog ecosystems.

Black-footed ferret habitat consists of biotic and abiotic components of prairie dog colonies (Coues 1877, Forrest et al. 1985). In addition to black-footed ferrets, prairie dog colonies host many vertebrate and invertebrate species, some in dependent relationships with prairie dogs, such as the black-footed ferret (Clark et al. 1982). This inter-relationship of plant and animal life centered on prairie dog colonies is often called the "prairie dog ecosystem" (Bureau of Land Management 1980). The ecology of prairie habitats in North America has been significantly altered over the past century because of the activities of man. Prairie dog ecosystems have been greatly affected by extensive poisoning over the last 100 years. As a result, many of these ecosystems were drastically reduced or totally eliminated. Many species dependent on prairie dogs have also suffered. Unfortunately, few data exist on actual prairie dog distribution and abundance prior to post-1915 poisoning campaigns by the Biological Survey and various states. The prairie dog ecosystems of today are perhaps the most notable exam-

ples of relict, insular ecological relationships. This is biologically significant because of the large numbers of associated species involved.

An understanding of historic data is essential for efficient management of such relict ecological relationships. This paper describes black-tailed prairie dog (*C. ludovicianus*) status in Montana from 1908 through 1914 and compares it with current knowledge about Montana prairie dogs and black-footed ferret habitat requirements as described in the literature. The historic extent and configuration of prairie dog colonies that determined black-footed ferret population sizes, densities and viability has not been previously described in the scientific literature.

METHODS

Data were derived from Northern Pacific Railway land surveys for 1908–1914. The study area was a belt up to 192 km wide and 483 km long, bisected by the Trans-Montana track, which entered Montana at Wibaux, extended west to Glendive on the Yellowstone

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River, then paralleled the river to Livingston. The Northern Pacific Railway, which formerly owned the Trans-Montana track, merged with other railroads to form the Burlington Northern, Inc., Railway in 1968. The Agricultural Resources Department, Burlington Northern, Inc., Miles City, Montana, provided the original survey data.

In Montana, the Northern Pacific was granted 20 odd-numbered sections of land per 1.6 km (1 mi) of track as inducement to link East to West by rail. Initially lands were se lected from a zone 32 km (20 mi) on either side of the track. However, because some sections were previously appropriated to homesteaders or other occupants, the government set a 96 km (60 mi) limit on each side of the track from which to select other sections. Three large exclusions within the 192 km strip were made for Northern Cheyenne and Crow Indian reservations and for high mountainous country. As a land grant railroad, the Northern Pacific partially funded track construction through disposition of some lands granted by the federal government.

Before Northern Pacific sold or leased land grant parcels, range examinations were made to map them and determine their present and potential land uses and existing natural re sources, including timber, grass, and water. Prior to 1908, the United States General Land Office had completed land surveys to mark section and quarter corners associated with the Montana Principal Meridian and Standard Parallel. As a result, the railroad land examiners accurately mapped topography, drainages, flatlands, timbered areas, coal outcrops, and other resource characteristics that influenced land value. Because prairie dogs were considered a menace that destroyed range land forage and crops, prairie dog colonies were also mapped.

The locations and extent of prairie dog colonies were indicated on original maps by writing "DOGS" or "DOG TOWN" across the occupied area, proportional to the size of the colony. For large colonies, letters appeared bold and widely spaced, and in some cases actual colony sizes were estimated. Often comments were included on prairie dog grazing effects or the spatial extent of colonies. Surveyed lands were mapped and color coded by estimated land use potential—grazing,

cropland, and woodlands, which indicated to pography and vegetation on which colonies were located. Herman Liebinger (personal communication to Wieland, 1979), land agent of eastern Montana land for the Northern Pacific Railway in the 1930s, was sure that all prairie dog colonies were recorded on all lands examined.

We designed data sheets to record the oc currence of prairie dogs from the original land assessment journals that recorded the sections [2.56 sq km (640 acres)] containing prairie dogs. For each section we recorded a "hit" or a "miss" for prairie dog occurrence. Hits and misses from the data sheets were color coded and plotted on mylar overlays of 1:250,000 USGS topographic maps. These overlays demonstrated the clustering of prairie dog colony distribution. For those sec tions with prairie dogs, an estimate was made from the maps as to how many 16 ha (40 acre) tracts (16 per section) contained prairie dogs. Furthermore, a given 16 ha tract could have anywhere from a few holes to an entire 16 ha of prairie dogs. We used the midpoint of 8 ha per tract to estimate colony sizes when actual sizes were not given. This gave us an estimate for actual size of prairie dog colonies. Since only odd-numbered sections were surveyed by the railroad, the method constituted a sampling procedure that amounted to a maximum 50% in those townships with complete coverage. Frequently prairie dog colonies extended an unknown distance beyond the boundary of the sample section.

RESULTS

The surveyed area encompasses a large portion of eastern Montana including parts of 22 counties (Fig. 1). The most prevalent land form is rolling sedimentary plains. Erosion coulees, river breaks, badlands, and intrusive mountain ranges are found throughout the area. Precipitation generally ranges from 30.5 to 40.6 cm per year, resulting in a shrub-grass steppe ecosystem. Upland sites support ex tensive stands of sagebrush (*Artemesia triden-tata*) and in some cases juniper (*Juniperus* sp.) or pine (*Pinus* sp.) woodland.

Black-tailed prairie dogs occupy the eastern two-thirds of Montana, or about 220,000 sq km (Hall 1981). Although prairie dog numbers
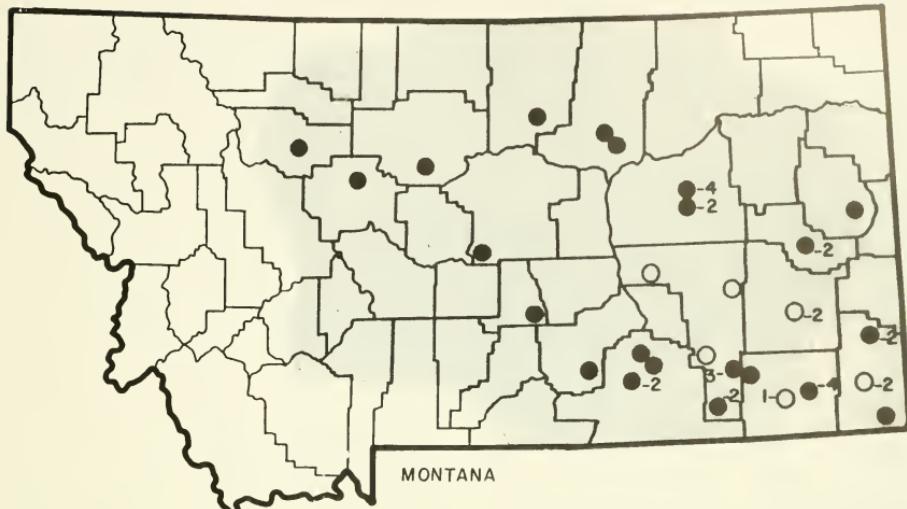
Fig. 1. Range of the black-tailed prairie dog (shaded area) and collection sites of black-footed ferrets (dots) in Montana. Specimens exist for solid circles.

have been greatly reduced, the extent of their overall range has changed little since the early surveys. The belt transect study area included about half of the total prairie dog range, with detailed land examinations of 17,052 sq km, or about 7.8% of the total Montana range of the species. This broad area includes steep terrain, shrubby vegetation, waterways, and intrusive mountain ranges that are not prairie dog habitat. The actual area occupied by prairie dogs throughout this large region was and is limited to relatively level areas, vegetated with herbaceous plants and few shrubs.

General George A. Custer's field journal on his travels to the Little Bighorn River in summer 1876 noted several extensive prairie dog colonies along Rosebud Creek (Fulton 1982). The railroad survey journals also describe many prairie dog colonies in this area. Colony sizes varied: some entries noted only a "few holes" per section surveyed, whereas others stated that a colony was large and extended over adjacent sections (e.g., T16N R45E S21 and to the southwest). We estimated the largest single colony at 9,328+ ha (23,040+ ac) near Beaver Creek and Sweeney Creek south of Hathaway (T4N R44E). Based on many such entries, our assessment of prairie

dog distribution should be considered a minimum estimate.

Prairie dog distribution based on the railroad surveys is given by county in Table 1. In the 22 surveyed counties, 6,661 sections within 759 townships were examined, representing 11.8% of the total area of these counties. Of the 6,661 sections, 1,662 (24.9%) were partially or totally occupied by prairie dogs. The largest area was in Rosebud County: of 1,025 sections examined, 397 contained some prairie dogs (38.7%). McCone, Park, Richland, Wheatland, and Wibaux counties all showed less than 10% of the sampled sections occupied by prairie dogs. Big Horn, Carter, Golden Valley, Musselshell, Powder River, and Treasure counties all showed some prairie dogs in more than 40% of the sampled sections. Based on the frequency distribution of colonies by sections, it seems that prairie dogs were relatively abundant and widespread, existing in single large colonies or in large groupings of smaller colonies.

The survey located 1,985 prairie dog colonies or one colony per 3.3 sections (Table 2). These colonies occupied all or part of 5,186 16 ha parcels, totaled a minimum of 475 sq km, and averaged 24.5 ha. Prairie dogs occupied a minimum 2.8% of the landscape.

TABLE 1. Black-tailed prairie dog distribution by county in Montana (1908–1914).

County	Square kilometers	Townships surveyed	Sections surveyed	Percent county	Sections with prairie dogs (%)	Percent 1976 land use[a] Rangelands	Crops	Woodlands	Other
Big Horn	1,946	7	27	0.5	18 (66.0)	84	9	6	1
Carter	1,305	13	146	4.4	59 (40.4)	89	7	3	
Custer	1,475	90	864	22.9	320 (37.0)	92	6	1	
Dawson	927	46	481	20.3	28 (5.8)	72	25		3
Fallon	634	40	321	19.8	51 (15.9)	76	22	1	
Fergus	1,695	3	7	0.2	0 (0.0)	64	20	15	
Garfield	1,754	66	810	18.0	109 (13.4)	93	4	2	
Golden Valley	458	13	164	14.0	69 (42.1)	83	10	5	
McCone	1,026	45	607	23.1	8 (1.3)	70	28		2
Musselshell	731	49	386	20.6	186 (48.2)	71	6	21	
Park	1,041	2	13	0.4	0 (0.0)	49	7	42	
Petroleum	645	15	81	4.9	50 (61.7)	93	4	2	
Powder River	1,284	31	311	9.4	132 (42.4)	84	5	10	
Prairie	677	49	389	22.4	39 (10.0)	88	11	1	
Richland	813	21	197	9.5	12 (6.1)	64	33		3
Rosebud	1,961	127	1,025	20.4	397 (38.7)	90	4	5	
Stillwater	700	8	26	1.4	4 (15.4)	59	20	19	
Sweet Grass	725	20	71	3.8	14 (19.7)	33	18	47	
Treasure	381	16	90	9.2	37 (41.1)	86	9	4	
Wheatland	554	23	225	15.8	5 (2.2)	87	6	6	
Wibaux	347	25	192	21.6	15 (7.8)	65	32	1	
Yellowstone	1,025	50	228	8.7	109 (47.8)	74	18	4	
Totals	22,105	759	6,661	11.8	1662 (24.9)	78	12	9	

a. Ross and Hunter (1976)

TABLE 2. Number of prairie dog colonies, number of 16 ha plots occupied, total estimated area occupied by prairie dogs, and mean colony size based on Northern Pacific Railway surveys (1908–1914).

Survey year	No. prairie dog colonies encountered	No. of 16 ha (40 ac) plots occupied by prairie dogs	Estimated hectares occupied by prairie dogs	Mean colony size (ha)
1908	174	743	10,031	57.6
1909	243	539	4,656	19.2
1910	600	1,735	14,812	24.7
1911	271	547	4,934	18.2
1912	56	105	672	12.0
1913	238	574	5,000	21.0
1914	403	943	7,464	18.5
Totals	1,985	5,186	47,568	24.5

To determine the clustering of prairie dog colony distribution, we sampled two belt transects through the study area. The east-west distribution of prairie dogs was sampled along a township-wide (9.6 km) belt transect (T4N) beginning at the Montana-North Dakota border (R61E) and running west to R15E (442 km). The south-north distribution of prairie dogs was also sampled using R45E from T5S north to T21N (240 km). Although sample sizes varied by township, 31 of the 47 townships (66%) along T4N contained prairie dogs and 14 of the 28 townships (50%) along R45E contained prairie dogs. Prairie dog colonies showed a markedly clumped distribution.

We defined a prairie dog colony complex as two or more colonies, regardless of size, in adjacent sections. Some complexes covered more than 36 contiguous sections (9,216+ ha). Maps of the two largest complexes in the sampled area are illustrated in Figure 3. Not all the area in Figure 3 was surveyed, but, of that portion surveyed, extensive prairie dog colony complexes appeared closely associated with river and stream courses. Many complexes extended 16 km or more. Along the Tongue River and Otter Creek, at least 20 complexes totaled an estimated 15,000+ ha. Mean intercomplex distance was about 3.4 km (range 1–7). Along the Powder River and O'Fallon Creek, at least 33 complexes occupied a very large area (estimated 20,000+ ha). Mean intercomplex distance was about 2.9 km (range 1–4).
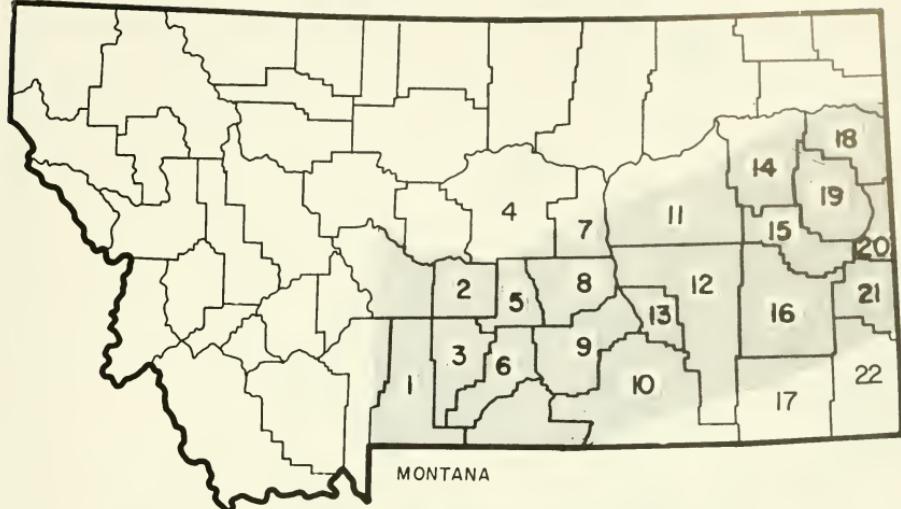
1 Park	7 Petroleum	13 Treasure	18 Richland
2 Wheatland	8 Musselshell	14 McCone	19 Dawson
3 Sweet Grass	9 Yellowstone	15 Prairie	20 Wibaux
4 Fergus	10 Big Horn	16 Custer	21 Fallon
5 Golden Valley	11 Garfield	17 Powder River	22 Carter
6 Stillwater	12 Rosebud		

Fig. 2. Location of the belt transect study area and counties surveyed.

Current land use in the survey area (Table 1) is for grazing livestock (78%), crop production (12%), and woodlands (9%). Other human uses (e.g., roads) represent only 1%. Land uses during 1908–1914 were probably similar to today's uses except for differences in fire suppression and cropping techniques. For example, in the past, more fires probably reduced woodlands and shrublands, thereby increasing availability of herbs and grasses for livestock use. Crop production has also changed because much crop-land today is extensively irrigated with technology unavailable in the early days. Furthermore, most homesteading within the study area took place from 1915 to 1917, just after the period we examined. Range conditions, which can affect prairie dog colonization and establishment, were not definitive by modern standards for the period 1908–1914 but were generally portrayed as conducive to increasing prairie dog populations.

We estimated changes in prairie dog distribution between 1908–1914 and today. The study area crossed a large portion of Montana and included about 92,736 sq km (over 40%) of the broad range of the black-tailed prairie dog in the state. Within the study area, 17,052 sq km were sampled. They contained an estimated minimum of 475 sq km of prairie dogs during 1908–1914. Assuming prairie dogs were distributed throughout the 220,000 sq km of known Montana prairie dog range like the distribution in the survey area, then at least 6,160 sq km of prairie dogs existed in the state at that time. However, deletion of several major intrusive mountain ranges from this calculation results in a historic estimate of 5,953 sq km of prairie dogs. Surveys from 1980 to date suggest about 506 sq km of prairie dogs, a 90+% reduction.

The drastic change in the status of the prairie dog ecosystem is also apparent when
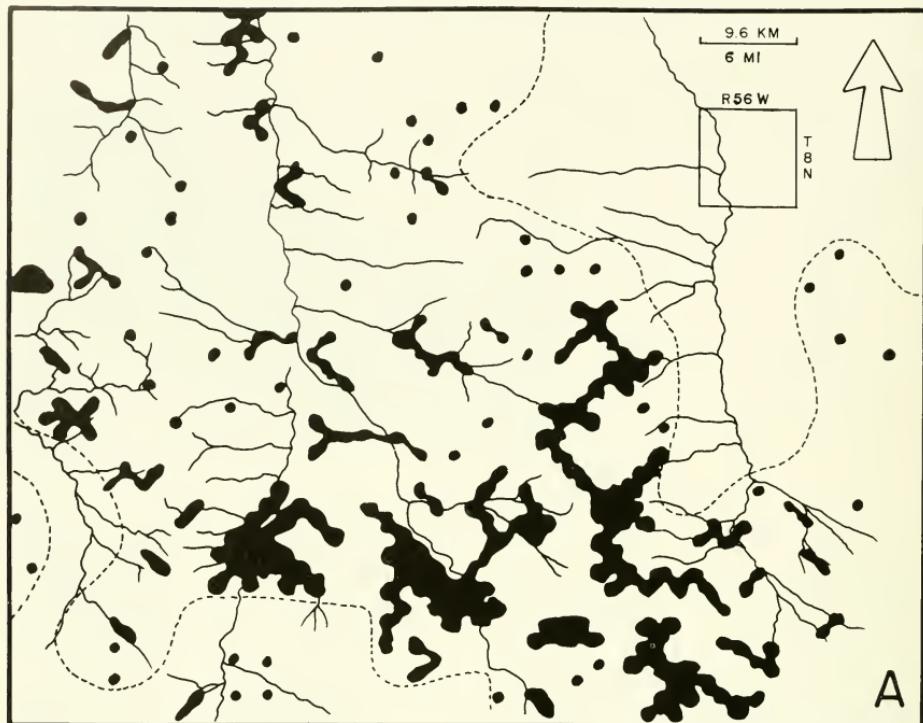
Fig. 3A. Prairie dog colony complexes in Powder River-O'Fallon Creek area, southeastern Montana (ca 1908-1914).

specific townships are compared between 1908–1914 and today. For example, one large prairie dog colony (at least 30 sections and 7,680 ha) in T4N R44E in Rosebud County 1908–1914 consisted in 1978 of only two small colonies totaling about 120 ha, only 2% of its original size. A sampling of five other townships for which specific data existed showed at least a 90+% reduction in prairie dog acreage.

DISCUSSION

Black-tailed prairie dog colonies, with their many associated and in some cases highly dependent invertebrate and vertebrate species, formerly occupied large areas of eastern Montana. Black-footed ferrets today are considered the rarest and most endangered mammal in Montana. Most known specimens (N=44) were collected between 1915 and 1953 from 15 counties in eastern Montana (Fig. 2). Reviewed by Anderson et al. (1986), these

records indicate that black-footed ferrets were widely distributed in Montana. The minimum estimated historic prairie dog range of 5,953 sq km scattered in suitable habitat over about 220,000 sq km represented a population distribution similar to that reported for other states during the 1908–1914 period (e.g., Nelson 1919, Seton 1929). Our estimates of prairie dog distribution in early Montana more closely approximate prairie dog distribution in presettlement times than prairie dog distributions seen today. Indeed, we estimate that current prairie dog distribution represents a remnant of probably 10% of the former pattern.

The greatly reduced extent of the prairie dog ecosystem resulted from poisoning campaigns that began in an organized way in 1915 under the Biological Survey and later under the U.S. Fish and Wildlife Service. No specific data were available on the annual extent of poisoning from 1915 to date for the
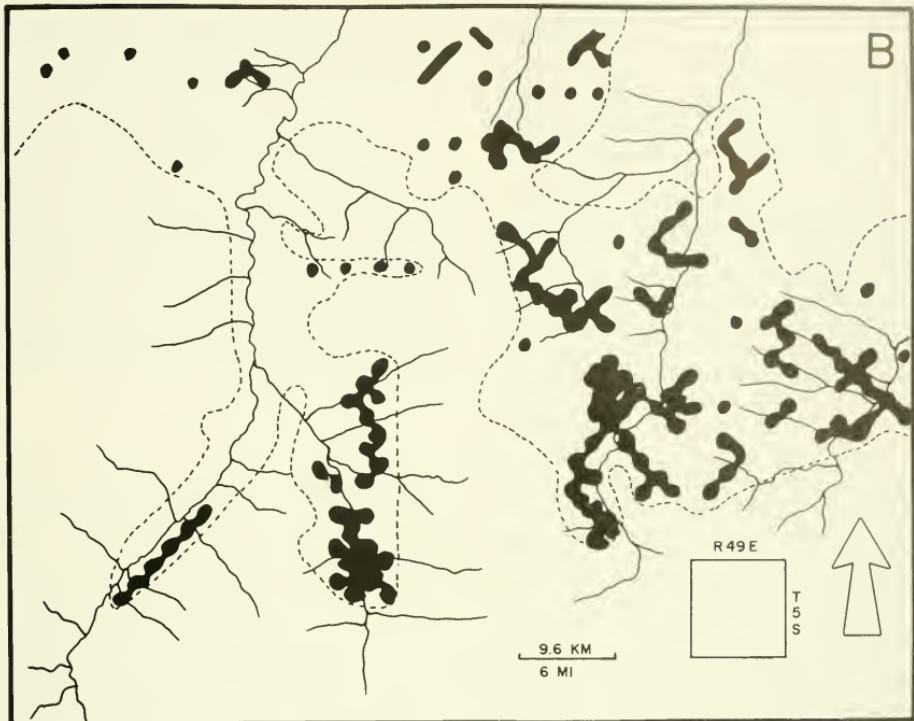
Fig. 3B. Prairie dog colony complex in Tongue River–Otter Creek area, southeastern Montana (ca 1908-1914).

study area. However, a chronological record of poisoning exists for Phillips County, just north of our study area. If Phillips County data are representative of the annual poisoning efforts for other parts of Montana, and there is every reason to believe that it is (e.g., Nelson 1919, Campbell and Clark 1981, Hubbard and Schmidt 1984), then a general chronology of reduction of the prairie dog ecosystem can be established.

The systematic poisoning program in Phillips County began in 1917. Over the next 22 years, 15,411 sq km of Richardson's ground squirrels (*Spermophilus richardsonii*) were poisoned with 168,486 kg of strychnine-soaked grain, and 69,652 ha of prairie dogs were poisoned with 34,109 kg of poison grain (Bureau of Land Management 1982). Because ground squirrels and prairie dogs often exist sympatrically, it is not possible in many cases to determine the target species for poisoning. Prairie dogs were poisoned on 27,530 ha in

1931, on 15,789 ha in 1932, and on 25,911 ha in 1933. Some of this effort was undoubtedly a second or third followup effort, but the extent of repeated poisoning of the same areas is unknown. By the end of 1933, reports mentioned that very few prairie dogs were left in the county. Limited poisoning continued until 1939, when it was felt the species was eliminated from the county. Various low-level poisoning efforts have continued irregularly to the present.

With the demise of prairie dogs went reductions in numerous other species, and the black-footed ferret serves as a dramatic example. If the black-footed ferret occurred at densities seen today in the Meeteetse, Wyoming, black-footed ferret area (1 black-footed ferret/ 57 ha) (Forrest et al. 1985), then at least 150,000+ individuals existed from 1908 to 1914 within the Montana prairie dog range. Direct elimination of habitat in some areas and a significant reduction and fragmentation

of habitat in other areas contributed directly to the reduction, or demise, of the black- footed ferrets. The sample areas for 1908–1914 reported in this paper along the Tongue and Powder rivers and Otter, Pump- kin, and O'Fallon creeks, for example, showed numerous prairie dog colony com- plexes 1.6–11.2 km apart (mean about 1.9 km). These historical Montana prairie dog ar- eas can be compared with the existing Mee- teetse, Wyoming, black-footed ferret/prairie dog complex, which is composed of 37 colonies totaling 2,995 ha (Forrest et al. 1985). Identification of this single complex recog- nizes that the size and distribution of black- footed ferret habitat islands is critical for the continued existence of black- footed ferrets.

Forrest et al. (1985) defined a "prairie dog complex" as a group of prairie dog colonies distributed so that individual black-footed fer- rets (and their genetic material) can migrate among them commonly and frequently. Within the Meeteetse complex, mean inter- colony distance is .92 km (range .13-3.70 km) and the mean black-footed ferret intercolony distance movement was 2.5 km. (5.7 maxi- mum). Early Montana prairie dog distribu- tions for 1908–1914 clearly fit the prairie dog complex definition of Forrest et al. (1985). Because of this, the historical Montana prairie dog situation undoubtedly served as high- quality black-footed ferret habitat. This con- clusion is further supported by our under- standing of black-footed ferret habitat requirements in South Dakota (Henderson et al. 1969, Hillman et al. 1979, Hillman and Clark 1980). The early Montana situation rep- resented a habitat setting in which black- footed ferrets evolved among the complex in- terrelationships of species and environmental interactions of the prairie dog ecosystem. The black-footed ferret's energetics, dispersal be- havior, predation avoidance, and litter pro- duction, for example, as seen in the Mee- teetse black-footed ferrets, seem well suited to a universe filled with numerous, large, closely spaced, and stable prairie dog colonies like those in south central Montana from 1908 to 1914 and probably earlier.

A few areas in Montana and in other states may still contain sufficiently large prairie dog complexes to support a black-footed ferret population and serve as examples of complex,

interactive prairie dog ecosystems. These ar- eas can be compared to the existing Meeteet- see black-footed ferret habitat (prairie dog complex) as described in Forrest et al. (1985). Their value for recovery can be assessed by using a comparative black-footed ferret habi- tat model such as that described by Houston et al. (1986). Prairie dog areas in Montana and elsewhere should be protected, as suggested by Hubbard and Schmidt (1984), as prairie dog refuges. Black-footed ferrets should be reintroduced into appropriate prairie dog refuges once they are described, management agreements are secured, and black-footed fer- rets are available for release.

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DESCRIPTION AND HISTORY OF THE MEETEETSE
BLACK-FOOTED FERRET ENVIRONMENT

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ABSTRACT.—The black-footed ferret (*Mustela nigripes*) occupied area lies in the western Big Horn Basin, Park County, Wyoming. Cody, a nearby town, shows a record high temperature of 40.5 C and a low of -43.3 C, with 173 days each year below 0 C. Area geology is dominated by Absaroka volcanics. Soils are shallow (0.5 m) and underlain by unconsolidated gravels; well-drained, medium-textured clay-loams (ca 1 m in depth); or clays derived from shale parent materials. Vegetation is characterized by a wheatgrass-needlegrass shrubsteppe type (*Agropyron/Stipa/Artemisia*). Prior to white settlement, the area hosted a diverse large mammal community. First white settlement began 1878–1885, with establishment of several area ranches. Predator and prairie dog (*Cynomys leucurus*) poisoning began about 1884. Heavy livestock grazing of public ranges followed the demise of bison (*Bison bison*) by 1890, which likely was conducive to a continuation of an ungulate-range relationship favoring prairie dog habitat. Ferret specimens from Crow Indian inhabitants of the region date to 1880s and two specimens from Park County date from the 1920s-1930s. Today ferrets are found on white-tailed prairie dog colonies (a "complex") totaling ca 2,995 ha. The areas occupied by these colonies are equally owned by private, state, and federal interests. Evidence shows many abandoned prairie dog colonies which, along with the current ones, total about 8,400 ha. Many of them may have been active simultaneously prior to poisoning in the 1930s.

This paper summarizes some physical and biological characteristics of the Meeteetse, Wyoming, black-footed ferret (BFF) environment, serves as a general description of the region, and provides a partial description of BFF habitat. It focuses on land uses, past and present, including prairie dog poisoning programs.

METHODS

A general description of the western half of Wyoming's Big Horn Basin (the general BFF study area) was obtained from numerous site visits between October 1981 and March 1985. Extensive conversations with ranchers, historians, anthropologists, state and federal wildlife managers, and literature reviews provided further understanding of the area. Prairie dog colonies in the general study area, which potentially serve as BFF habitat (Linder et al. 1972, Hubbard and Schmidt 1984, Anderson et al. 1985, Forrest et al. 1985), were located by air and ground surveys and interviews with landowners. Summer spotlighting surveys and winter snow-tracking surveys determined the distribution of BFF-occupied prairie dog colonies. An intensive

study area was delineated within the larger study area from these data. All prairie dog colonies were mapped on 1:62500 USGS topographic quads. BFF-occupied colonies were mapped on 1:4800 base maps we prepared to detail site features. Historical information was obtained from the literature and interviews with area ranchers and participants in prairie dog poisoning programs. "Dead" prairie dog colonies were identified by the presence of unused, revegetated prairie dog mounds as described by Clark (1970).

THE ENVIRONMENT

The Meeteetse study area is named after a small community in the Big Horn Basin of northwestern Wyoming (Fig. 1). The larger extensive study area includes most of the western half of the Basin (8,000 sq km) including parts of Park, Hot Springs, Big Horn, and Washakie counties. The Basin is enclosed by mountains on the west, south, and east and is open to the north. The Shoshone, Greybull, and Bighorn rivers drain the Basin. The smaller intensive study area containing the BFFs is also shown in Figure 1. Portions of the larger study area have been described by the

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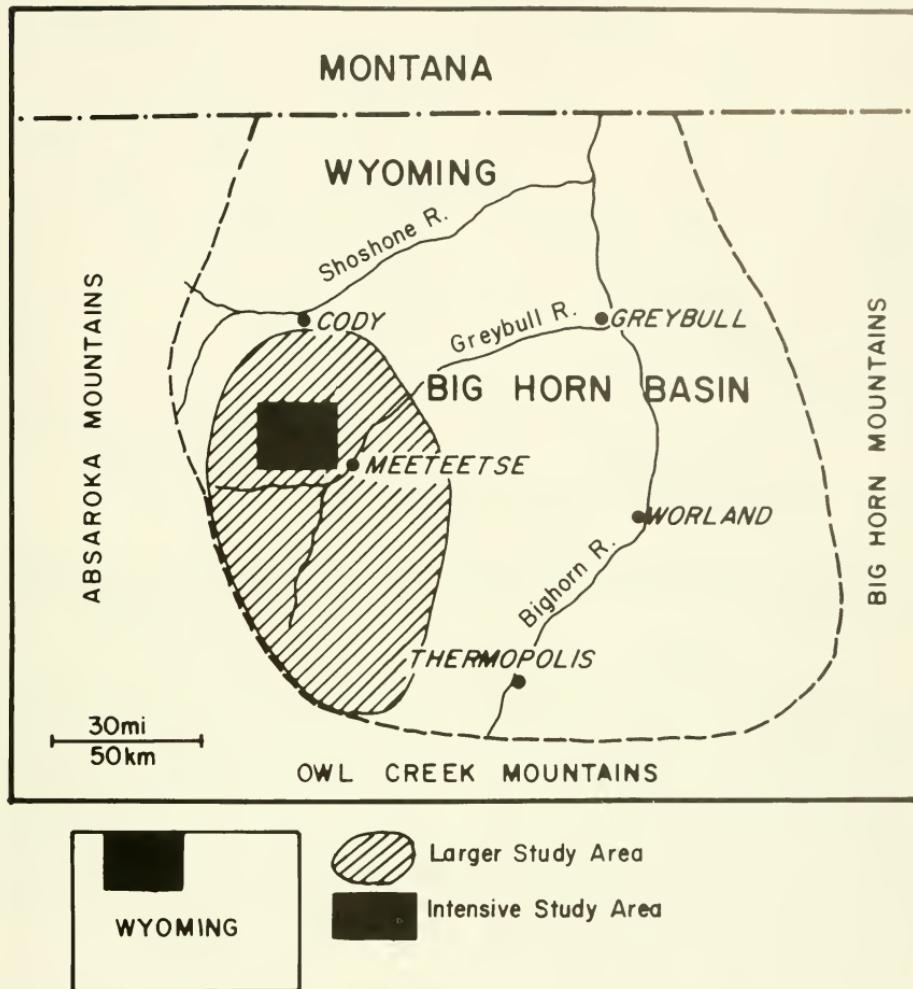
Fig. 1. Location of the larger and intensive black-footed ferret study areas in the Big Horn Basin of northwestern Wyoming.

U.S. Forest Service (1982) and the U.S. Bureau of Land Management (1982). The intensive study area and ferret use of that area were described by Forrest et al. (1985) and modeled by Houston et al. (1986).

Climate

Climatographs for Cody, Wyoming, located north of the intensive study area, and Thermopolis, Wyoming, at the south end, are shown in Figure 2. The record high temperature for Cody is 40.5 C and the record low is -43.3 C, with 173 days each year below 0 C based on 1960 U.S. Department of Commerce records. The Thermopolis record high is 41.1 C and the low is -41.1 C with 194 days below 0 C. Winds are estimated to average 13–16 kmph at Cody, with lower velocity winds at Thermopolis. The Meeteetse area is generally snow-free, because of wind action. Occasional accumulations, generally 10 cm or less, may occur for several days at a time.
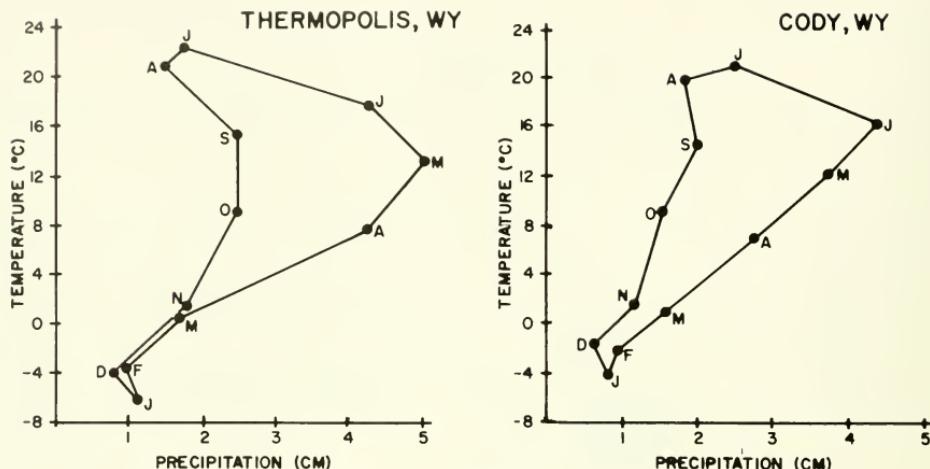
Fig. 2. Climatographs for Cody and Thermopolus, Wyoming (1931–1960).

Prevailing winter winds are westerly. Mean annual isohyets for the Big Horn Basin are shown in Figure 3.

Geology

Area geology is dominated by Absaroka vol- canics that compose most of the Absaroka Range and Carter Mountains immediately west of the study area. Surface geology is de- scribed by Pierce (1978) and shown in Figure 4. Most prairie dogs are associated with Cody shales or unconsolidated sediment. Prairie dog association with shale-derived soils has been identified in other studies (Stromberg 1975, Knowles 1982). Shale parent materials may provide clayey soils that are structurally more stable for burrow construction.

Known geological structures for oil and gas in the region are shown in Figure 5. Oil and gas potential for much of the intensive study area is rated high (U.S. Forest Service 1982). Following discovery of the BFFs, 41 mineral leaseholders were notified in March 1982 of possible changes in lease status by the U.S. Bureau of Land Management. The affected area included about a 1 km buffer zone around the intensive study area.

Soils

Soils are shallow (0.5 m and underlain by unconsolidated gravels); well drained, with medium-textured clay-loams (ca 1 m in depth); or clays derived from shale parent materials. Additional soil descriptions are given by Collins and Lichvar (1986).

Vegetation

Vegetation is characterized by Kuchler's (1964) description of wheatgrass-needlegrass shrubsteppe type (*Agropyron/Stipa/Artemisia*). Vegetation of the intensive study area is dominated by *Koeleria cristata*, *Agropyron spicatum*, *A. smithii*, and mixed shrub (largely *Artemisia tridentata*) as described by Collins and Lichvar (1986). Vegetation has been heav- ily grazed by cattle, horses, and sheep for about 100 years.

Prairie Dogs

Current prairie dog distribution within the intensive study area is shown in Figure 6. The 37 colonies shown total 2,995 ha and contain about 125,000 prairie dog burrow entrances. BFF occupancy has been noted in 23 of these colonies. Prairie dog burrow openings aver- age 41.7 per ha, and prairie dog densities reach 9 per ha (Clark et al. 1985). BFF use of these colonies is described by Forrest et al. (1985).

Surface and subsurface ownership is pre- sented in Table 1. Surface ownership is about equally divided among state (31.0%), federal (33.4%), and private (35.6%) entities. Subsur- face ownership is 57% federal, 31% state, and
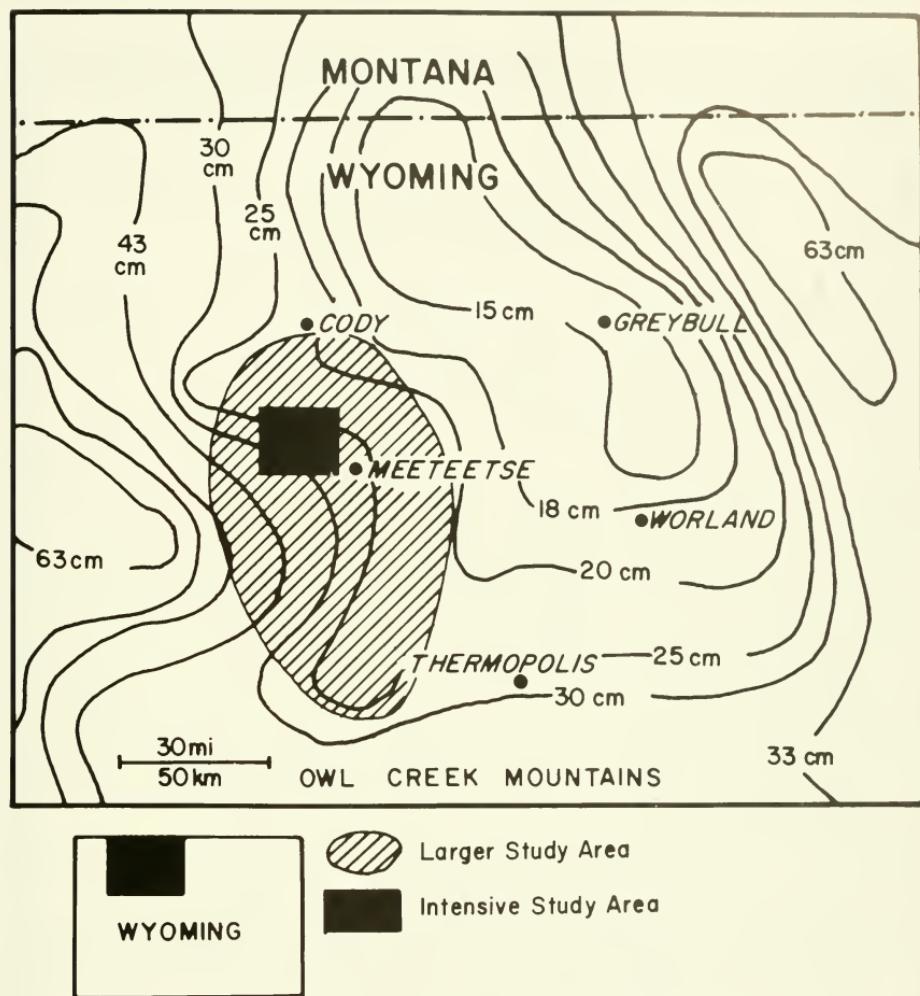
Fig. 3. The mean annual isohyets for the Big Horn Basin of northwestern Wyoming showing the larger and intensive black-footed ferret study areas and major towns.

12% private. Seven ranches contain BFFs, with about two-thirds of the total prairie dog colony area on one ranch. The other six ranches each have 1%-9% of the total BFF area.

Comparisons of the Meeteetse area with eight other prairie dog study areas are shown in Table 2. Ten variables are contrasted among these areas. The Meeteetse BFF/ prairie dog site falls within ranges for these variables, except that it shows a greater mean

burrow opening density and lower inter-colony distance than the other areas. Unfortunately, data are not complete in all cases for comparative purposes.

Land Use History

The Big Horn Basin was opened to white settlement in the mid-1870s. Previously the area was used as hunting and wintering ground by Mountain Crow Indians, whose major impact was likely restricted to occa-
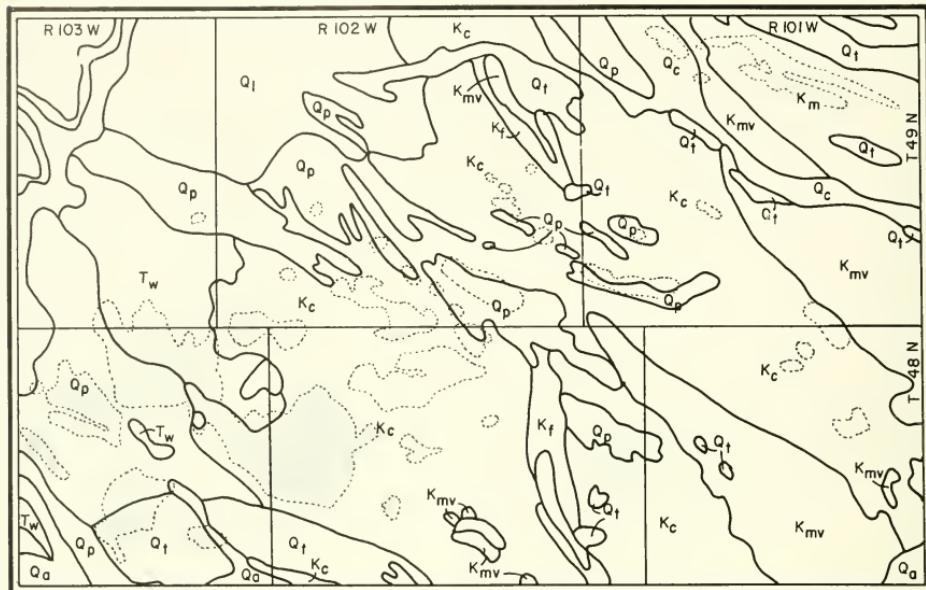
Fig. 4. Geological map of the intensive black-footed ferret study area showing prairie dog colonies in relation to underlying geology.

K_c —Cody Shale (Upper Cretaceous)—Upper part buff sandy shale and thinly laminated buff sandstone. Lower part dark-gray, thin-bedded marine shale. Thickness 500–1000 m.

Q_p —Pediment deposits—Thin veneer of poorly rounded to subangular surficial material deposited on smooth, gently sloping erosion surfaces cut in bedrock.

Q_t —Terrace gravel—Unconsolidated deposits of gravel, sand, cobbles, and silt.

K_{mv}—Mesaverde Formation (Upper Cretaceous)—Interbedded light gray sandstone and gray shale in upper part; lower part massive lightbuff, ledge-forming sandstone containing thin, lenticular coal beds.

K_f —Frontier Formation (Upper Cretaceous)—Thick lenticular gray sandstone, gray shale, brown carbonaceous shale and bentonite. Torchlight sandstone.

K_m —Meeteetse Formation.

Q_a —Alluvium—Unconsolidated deposits of silt, sand, gravel, and cobbles along stream valley and at or near present stream level. Includes alluvial fans and glacial outwash.

Q_c —Colluvium—Heterogeneous deposits of rock detritus.

Q_l —Landslide deposits—Heterogeneous deposits of rock debris emplaced by mass movement.

T_w —Wapiti Formation (Eocene)—Dark-brown andesitic breccia, tuff, volcanic sandstone, siltstone, and conglomerate; lava flows and flow breccias; dark to medium-brown pyrozene andesite; sparse horneblende. Includes predominantly volcanic sandstone and siltstone of the Pitchfork formation of the Sunlight Group of the Absaroka Volcanic Supergroup in upper Greybull River area. Thickness 1000–1500 m.

sional ground fires (Edgar and Turnell 1978). During 1878–1885 several area ranches were established, most notably the Pitchfork Ranch founded by Otto Franc. The Pitchfork Ranch grazed about 15,000 head of cattle on various ranges throughout the Basin by 1884, encompassing virtually all the lands in the intensive BFF study area (Edgar and Turnell 1978). The Pitchfork Ranch incorporated surrounding ranch properties in the period 1903–1922, en compassed 100,000 ha, and grazed 12,000– 20,000 head of cattle and 60,000 head of sheep.

As D. Healy (in Killough 1977) points out, estimates of range use during the open range period are difficult to assess, and little experi ence concerning the productivity of fenced allotments was available prior to the passage of the Taylor Grazing Act in 1934. Carrying capacity estimates were likely too optimistic, resulting in heavy overuse of public range. Killough (1977) states that this probably oc curred throughout the Bighorn Basin. By the 1930s the Pitchfork was grazing about 20,000 sheep and 5,000 cattle on 28,000 ha of deeded land, 44,000 ha of leased land, and 24,000 ha
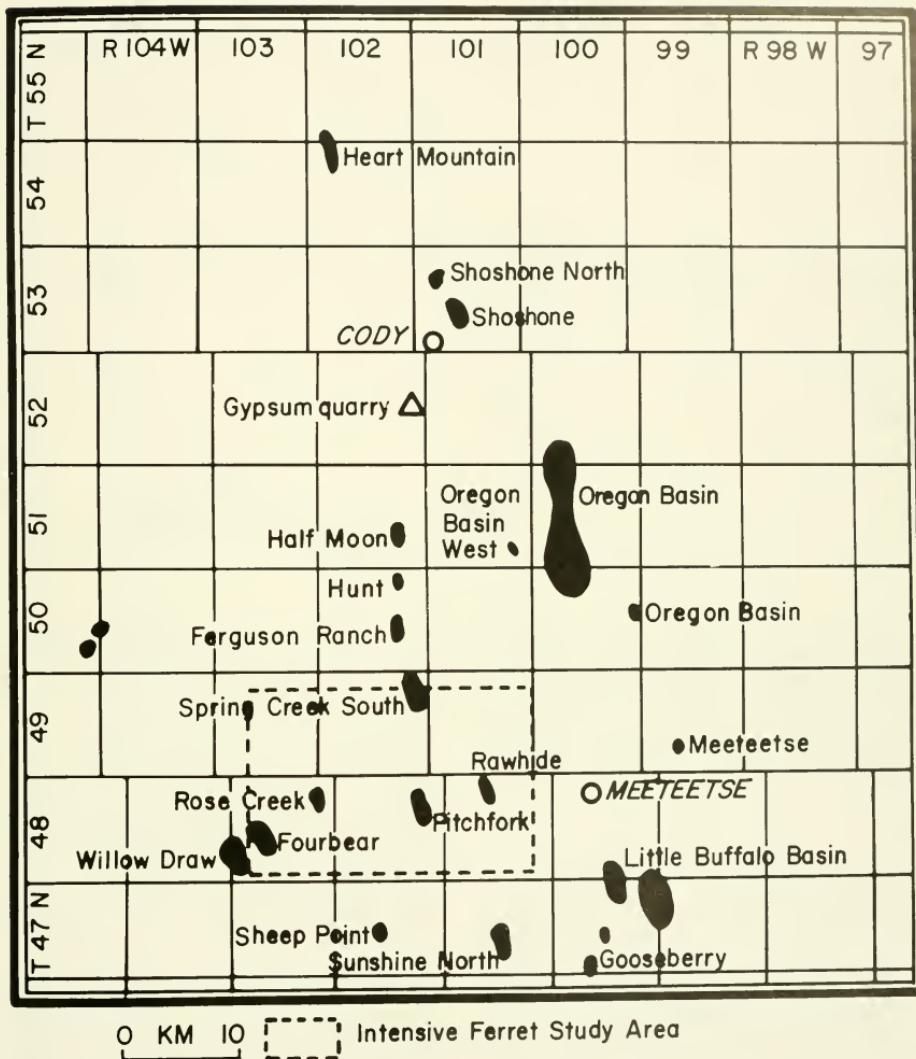
Fig. 5. Map of oil and gas fields and mining regions for the western Big Horn Basin in relation to the intensive black-footed ferret study area.

of permitted land (Turnell 1982, personal communication). The LU Ranch on Grass Creek, south of Meeteetse, which had poorer range conditions, controlled a comparable 100,000 ha and grazed 1,500 cattle and 15,000 sheep (Killough 1977).

Oil activities, beginning in the 1950s, included seismic testing for underlying geological structures and a concomitant increase in primitive roads to maintain wells, pipelines, and support facilities. In recent years seismic activity has increased within the intensive
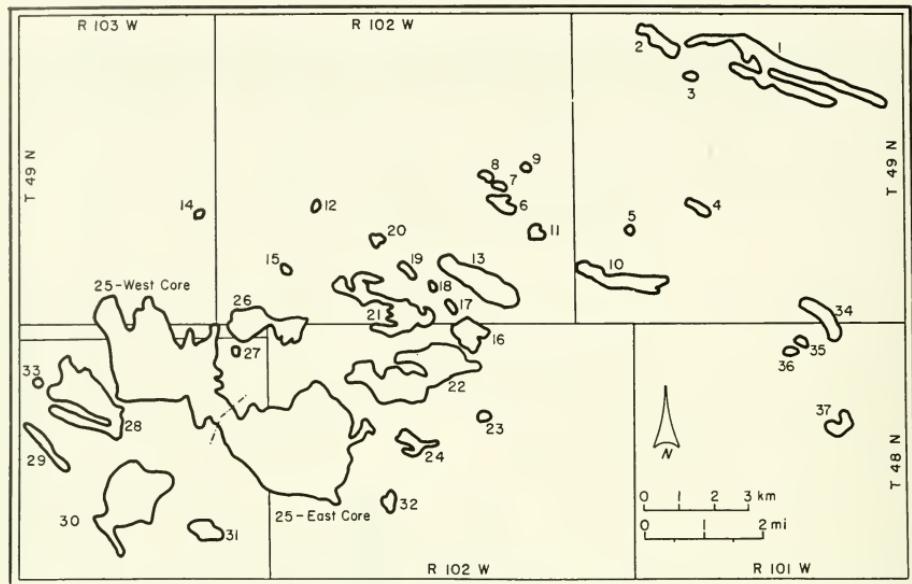
Fig. 6. Prairie dog colonies in the Meeteetse intensive black-footed ferret study area.

study area. In 1981 prior to discovery of the BFF population, four wells were drilled on the Rose Creek Field directly on the largest BFF concentration (Fig. 5). In addition, two subsurface pipelines and one pumping station are located in BFF-occupied prairie dog colonies.

Fauna

Prior to white settlement, the area probably hosted a diverse faunal assemblage dominated by grazing ungulates and their various predators. Killough (1977) found bison skulls exposed as deep as 3.6 m in gullies in the Big Horn Basin, showing long-term use of the area by bison and suggesting that periods of overgrazing and erosion followed by range restoration (gully healing) may have been common within recent history. White trappers recorded large bison herds in the upper Greybull drainage as late as 1878. James White, who worked in the Greybull River country, secured 2,000 hides in 1880 alone (Edgar and Turnell 1978). The last locally known native bison was killed along Meeteetse Rim in 1892 (Edgar and Turnell 1978). Although bison skeletal remains were inten-

sively scavenged for fertilizer markets throughout the West, numerous bones and horn sheaths can still be found in this area today.

Otto Franc recorded the presence of literally thousands of bighorn sheep (*Ovis canadensis*) wintering along the Greybull in 1880, and Archibald Rogers noted on a hunting trip to the -TL Ranch (later Pitchfork) in 1893 a band of 250 bull elk (*Cervus ela-phus*)(cited in Egdar and Turnell 1978). By 1890 Franc noted a drastic decline in big game numbers from a decade of unchecked exploitation by sport, skin, and market hunters. Big game numbers continued to decline in the area through the early 1900s, although pronghorn (*Antilocapra americana*) were protected on Pitchfork Ranch lands and occasionally transplanted elsewhere. Big game numbers have experienced an apparent recovery and have continued to increase since a low during the 1940s (J. Lawrence and J. Turnell, personal communication). Grizzly bears (*Ursus arctos*) were apparently quite common, as records of bear encounters abound (e.g., Seton 1899). By 1894, gray wolves (*Canis lupus*) began depredations on live-

TABLE 1. Size, surface, and subsurface ownership patterns of prairie dog colonies in the intensive black-footed study area.

Colony number	Colony name	Colony size (ha)[2]	Surface ownership State %	Surface ownership Federal %	Surface ownership Private %	Subsurface ownership State %	Subsurface ownership Federal %	Subsurface ownership Private %
1	Long Hollow Corrals	196.5	75	—	25	75	5	20
2	Long Hollow West	26.5	—	65	35	—	100	—
3	Long Hollow South	2.5	85	—	15	85	15	—
4	Lot 58	12.5	100	—	—	100	—	—
5	Section 30	1.5	—	100	—	—	100	—
6	Rush Creek Basin	24.0	—	70	30	—	70	30
7	Rush Creek B	3.0	—	—	100	—	—	100
8	Rush Creek C	8.5	—	—	100	—	—	100
9	Rush Creek D	5.0	—	—	100	—	—	100
10	BLM 10	49.5	—	—	100	—	100	—
11	BLM 14	20.5	—	100	—	—	100	—
12	Little Rawhide West	0.5	—	—	100	—	100	—
13	BLM 13	183.0	20	80	—	20	80	—
14	Rawhide West	0.5	—	—	100	—	—	100
15	Westbrook Draw	2.5	100	—	—	100	—	—
16	Lower BLM	50.5	—	85	15	—	48	52
17	Little Rawhide #1	1.0	—	100	—	—	100	—
18	Little Rawhide #2	2.0	—	100	—	—	100	—
19	Little Rawhide #3	6.0	—	—	100	—	—	100
20	Little Rawhide Basins	9.0	60	—	40	60	40	—
21	Rawhide	102.0	7	3	90	7	3	90
22	Pump station	230.0	—	45	55	—	65	35
23	Tonopah	31.5	—	100	—	—	100	—
24	Thomas	31.5	—	—	100	—	100	—
25 EAST	East Core	738.5	—	47	53	—	100	—
25 WEST	West Core	568.5	80	11	9	80	14	6
26	91 Town	97.5	75	—	25	75	8	16
27	Fence	0.5	—	—	100	—	100	—
28	Rose Creek	158.0	75	—	25	75	25	—
29	Island	21.0	100	—	—	100	—	—
30	Pickett Creek	211.0	5	85	10	5	85	10
31	Graveyard	51.5	60	—	40	60	—	40
32	Hogg	30.5	—	100	—	—	100	—
33	Rose Creek West	9.5	100	—	—	100	—	—
34	Spring Creek Basin A	69.5	—	—	100	—	100	—
35	Spring Creek Basin B	3.5	—	—	100	—	100	—
36	Spring Creek Basin C	11.0	—	—	100	—	100	—
37	Spring Creek Basin D	24.5	—	—	100	—	100	—
Total		2995.0						

stock, possibly as a result of decimated large mammal populations. Wolf predation concerned Franc until his death in 1902 (Edgar and Turnell 1978), and Mrs. H. C. Larsen of Wood River also noted that wolves were numerous from the late 1800s until the 1920s (Diem 1973).

The historic relationship between prairie dogs and bison can only be surmised, although the role of bison in grassland ecosystems has been debated for some time (Larson 1940). Nevertheless, there is little doubt that there was a reciprocal ecological relationship between bison and prairie dogs, each tending to maintain the shortgrasses interspersed with patches of forbs, ideal habitat for each other (Koford 1958). Osborn and Allen (1949) and King (1955) also noted that bison tended to concentrate on prairie dog colonies, their activities apparently creating an environment that favored prairie dogs. These bison activities included "over grazing," trampling soil, wallowing, and defecating and urinating. In the late 1850s, Mead (1899) noted that prairie dogs disappeared from parts of Kansas shortly after the bison and concluded that bison were

TABLE 2. Some physical characteristics of white-tailed prairie dog colony complexes near Meeteetse, Wyoming, compared to other prairie dog complexes in Wyoming and Utah.

Characteristics	Meeteetse WY (this study)	Medicine Bow WY (Campbell & Clark 1981)	Vernal UT (Clark et al. 1982)	Cisco UT (Clark et al. 1982)	Polecat Bench NW WY (Clark 1977)	Cumberland Flats SW Wyoming[1]	South Central Wyoming[2]	South Central Wyoming[3]	Totals or Means
Study area size (km²)	333	336	1886	298	128	256	556	483	534.5
Number of colonies	37	25	18	15	4	63	164	81	388
Total area of colonies (ha)	2995	1085	3584	566	3020	3969	4008	4298	23,388
Percent of study area	9.0	3.2	1.9	1.9	2.3	15.5	7.2	8.9	6.2
Number of ha of dogs/100 km²	899	320	190	190	2359	1550	720	890	884.6
Number of colonies/100 km²	11.1	7.4	1.0	5.0	3.1	24.6	29.5	16.8	11.1
Colony size (ha):									
Mean	80.9	43	199	38	755	63	24	53	163.2
SD	217.2	46.4	249	37	—	—	—	—	—
Range	0.5–1307	2–184	0.2–958	9–121	120–1400	0.4–2000	0.8–510	—	—
Number of burrow openings examined	125,000	24,620	76,579	8,993	6,775	168,761	105,497	129,969	630,049
Burrow openings/ha:									
Mean	41.7	25.1	30.8	19.8	2.1	43	4	30	26.5
SD	62.1	26.4	37.6	10.2	—	—	—	—	—
Range	13.7–290.7	9–129	5.1–160	2.3–40.5	—	4.2–130	0.8–41	—	—
Intercolony distance (km):									
Mean	0.9	1.5	4.4	5.5	—	—	—	—	—
SD	0.78	1.0	—	—	—	—	—	—	—
Range	0.06–3.1	0.4–3.6	0.8–11.3	0.8–11.3	—	—	—	—	—

[1]Clark et al. 1982; Martin and Schroeder 1979, 1980.
[2]Martin and Schroeder 1979.
[3]Martin and Schroeder 1980.

necessary for prairie dog existence because they compacted soils and created communities of forbs.

Clark (1973) presented a model hypothesizing the interrelationship of bison and prairie dogs, in which both animals functioned in a reciprocal manner ecologically to increase grassland productivity beyond what each species could contribute individually. More recently Bonhan and Lerwick (1976), O'Mellia et al. (1980), Uresk and Bjugstad (1980), and Coppock et al. (1983) have studied prairie dog ecology and, in some instances, prairie dog-bison relationships. Their results support the earlier observations and models described above. When large numbers of domestic live-stock replaced the bison at the turn of the century, they may have continued to provide an environment conducive to prairie dog oc-cupancy of the Meeteetse area.

Historic Ferret Habitat

Because BFFs require prairie dogs as part of their habitat, a review of historic prairie dog status and poisoning programs in the region pro-vides data on historic BFF habitat. BFFs have most likely occupied the Meeteetse area and Big Horn Basin since pristine times. Crow Indians of the region collected BFFs as medicine objects in the mid- to late 1880s (Clark 1975). Clark (1977) listed 20 BFF reports from the Big Horn Basin from 1889 to 1977. Two of these reports originated in Park County, in the vicinity of the intensive study area. Ed Larson and Frank Smith, oldtime residents of Meeteetse, report trapping or knowing of trapped BFFs in the 1920s-1930s from the Meeteetse Creek area. Cal Todd, former manager of the Pitchfork Ranch, and his wife, Margo, reported that their dog killed a BFF in 1962 on the headquarters grounds. The corpse was described to George Reesy, Wyoming Game and Fish Department, who did not investigate it. The skin was retained for about 6 yrs and later lost. In September 1981 a male BFF was killed by a dog on the John Hogg Ranch (Clark and Campbell 1981). Subse-quently, a nearby BFF population was located by Doug Brown, a cowboy, which lead to the present study.
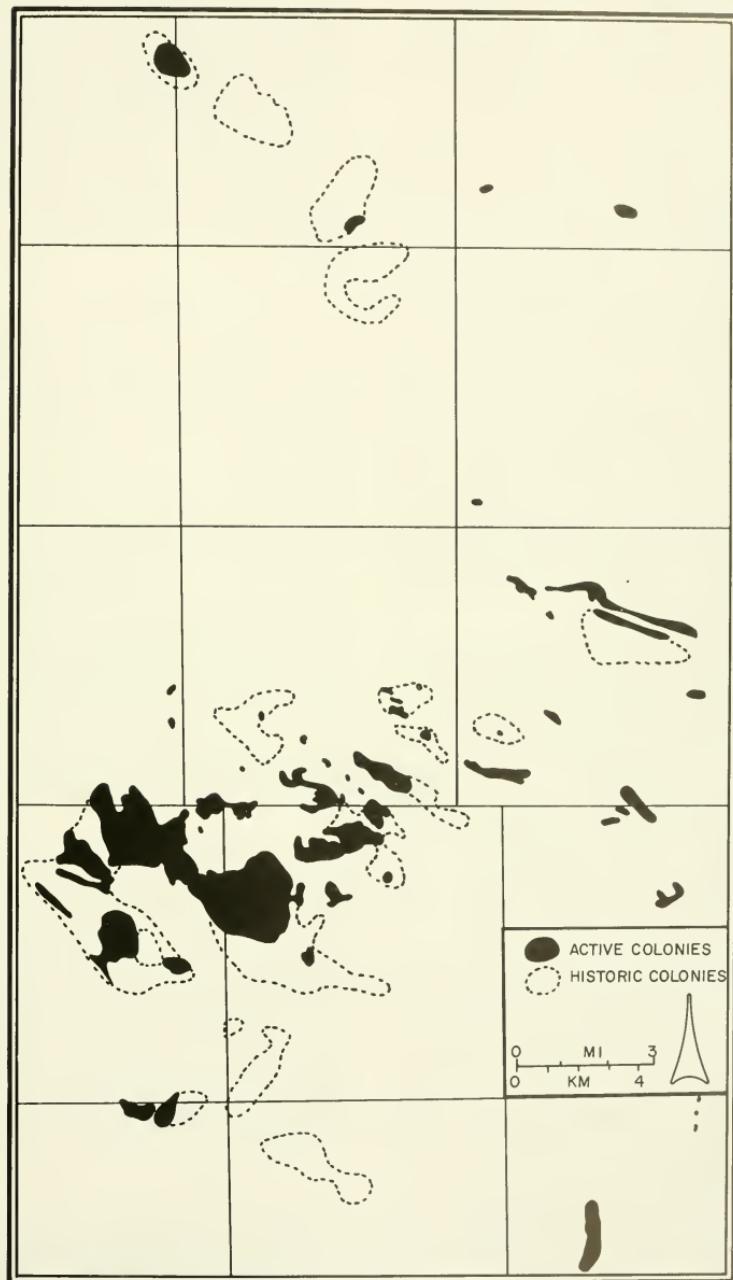
Fig. 7. Location of currently active and historic "dead" prairie dog colonies, near Meeteetse, Wyoming, 1984.

Prairie dog control programs within the in tensive study area began in the 1880s (Edgar and Turnell 1978) and continued sporadically until the mid-1930s. From 1923 to 1928 ro dent control expenditures for Park County totalled $7,476, the third highest county ex penditure in the state. During the same pe riod more than 500,000 ha of prairie dogs were eradicated in Niobrara, Weston, and Camp bell counties (Day and Nelson 1929), so con siderable control activity was occurring. Over a five-year period during the mid- to late 1930s, large and well-organized poisoning programs were conducted throughout most, if not all, of the intensive and general study areas (B. Sells, E. Larson, F. Smith, personal communication). All of Meeteetse, Rush, Rawhide, and Spring creeks, and parts of the Greybull and Wood River drainages were poi soned, as well as much of the area north of Meeteetse Creek up to Cody. These federal programs poisoned only a portion of the total area during any one year, and, even though "kill rates" are undocumented, 50%-100% kills of prairie dogs were often obtained else where (e.g., Tietjen 1976).

The entire prairie dog complex was appar ently never all poisoned in a single year. Be ginning in the 1940s and continuing through the 1960s, limited poisoning was carried out on specific colonies or areas (B. Rosan, J. Win ninger, D. Winninger, J. Turnell, J. Hogg, personal communication). This suggests that the 1930s campaigns were effective in elimi nating prairie dogs, leaving few to be poi soned later (M. Todd, personal communica tion). This pattern has been seen in other areas where adequate data exist, such as Phillips County, Montana (Bureau of Land Management 1982) and in eastern Wyoming (Clark 1973, Campbell and Clark 1981). Since 1970 only a few small areas have been poi soned (J. Hogg, J. Winninger, J. Turnell, A. Thomas, B. Gould, personal communication).

Since "dead" prairie dog colonies may retain their identity for 60+ years (Clark and Camp bell, unpublished data), we used areas for merly occupied to get a maximum upper size (after Clark 1970) of the prepoisoning colony complex. We assumed that all the "dead" prairie dog colonies seen today were simulta neously active prior to the large 1930s poison ing campaigns, plus those colonies currently

active. The estimated total of 8,400 ha of colonies may have been present prior to the 1930s (Fig. 7). If one assumes that these 8,400 ha of prairie dog colonies could support one BFF for each 50 ha (Forrest et al. 1985), then a maximum estimate of the pre-1930s BFF pop ulation in the pre-1930s can be obtained. As suming all else is equal between today's ob served BFF population size, density, and reproductive rate, the pre-1930 BFF habitat could have supported as many as 168 adult BFFs.

DISCUSSION

The overall climate, geology, soils, vegeta tion, and land use history of the Meeteetse area, which today contains the world's only known BFF population, is similar to much of Wyoming and other areas throughout the West where prairie dogs are found. BFFs probably always inhabited the Meeteetse re gion. Their persistence there today is proba bly due to: (1) a historical abundance of prairie dog habitat, (2) prairie dog control programs that left active colonies or parts of colonies unpoisoned during any one year, and (3) ab sence of catastrophic diseases (sylvatic plague, distemper). Prairie dogs were apparently kept at low levels after the 1930s, and this "bottle neck" for BFFs persisted for some years, per haps having genetic consequences for the BFFs of today (Pettus 1985, Kilpatrick et al. 1986).

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VEGETATION INVENTORY OF CURRENT AND HISTORIC
BLACK-FOOTED FERRET HABITAT IN WYOMING

Ellen I. Collins[1] and Robert W. Lichvar[2]

ABSTRACT.—A vegetation inventory of current and historic black-footed ferret (*Mustela nigripes*, BFF) habitat was completed in the 1983 growing season. White-tail prairie dog (*Cynomys leucurus*) colonies near Meeteetse, Wyoming, provide the only known BFF habitat. Four other prairie dog complexes located in Wyoming, documented historic BFF habitat, were also inventoried. Prairie dog burrows occur in two of eight vegetation types present in the current BFF habitat study area. They are junegrass (*Koeleria cristata*) and sagebrush/junegrass (*Artemisia tridentata/ K. cristata*; named for dominant species). In historic BFF habitat, prairie dog burrows occur in six vegetation types: birdfoot sagewort/western wheatgrass (*Artemisia petadifida/Agropyron smithii*), alkali sagebrush (*Artemisia longiloba*)/ mixed grass, Gardner saltbush (*Atriplex gardneri*)/ mixed grass, and thickspike wheatgrass-threadleaf sedge (*Agropyron dasystachyum-Carex filifolia*), mixed shrub/mixed grass, and Gardner saltbush. Similarities among all five complexes are plant heights generally less than 66 cm, level to gently rolling topography, and severe disturbance due to historical grazing, vegetation manipulation, and other human-related activities. Of the vegetation parameters measured, only plant height appears to be important to white-tail prairie dog distribution. White-tail prairie dog colonies do not appear to depend on a particular vegetation type; consequently, vegetation type alone should not be used to identify BFF habitat.

A comparative vegetation inventory including cover, shrub density, and plant height measurements with qualitative field observations of current and historic BFF habitat was completed in summer 1983. This study was conducted as part of a comprehensive program designed to identify parameters important to the selection of potential BFF relocation sites. This paper presents results of the study.

TABLE 1. Location of five study sites in Wyoming.

White-tail prairie dog complex	County	Legal location
CURRENT FERRET HABITAT		
1. Meeteetse complex		
Core Colony[1]	Park	T48N R102W; T48N R103W
91 Colony	Park	T48N R102W; T48½N R102W
Pickett Creek Colony	Park	T48N R103W
Thomas Colony	Park	T48N R102W
Lower Bench Colony	Park	T48N R102W; T49N R102W
Tonopah Colony	Park	T48N R102W
Pump Station Colony	Park	T48N R102W
BLM-13 Colony	Park	T49N R102W
Island Colony	Park	T48N R103W
Graveyard Colony	Park	T48N R103W
Timber Creek Colony[2]	Park	T48N R102W; T47N R102W
(abandoned)		
HISTORIC FERRET HABITAT		
2. Larsen's Ranch Complex	Sweetwater	T22N R93W
3. Wasmer Flats Complex	Uinta	T16N R118W
4. Gillies Draw Complex	Park	T47N R98W; T48N R98W
5. Horne Flats Complex	Carbon	T22N R78W; T21N R78W

[1]Prairie dog colony names follow Forrest et al. (1985).
[2]No evidence of BFF occupancy 1981–1984; probably poisoned and abandoned in 1960s.

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TABLE 2. Summary comparison of important descriptive parameters for the five study sites.

Prairie dog complex	Vegetation type	Total cover (%)	Shrub density (stems/m^2)	Plant height (cm)	Elevation (m)	Topography
CURRENT FERRET HABITAT					2134–2256	Rolling hills and flat benches
1. Meeteetse Complex						
Core Colony	Junegrass	73	0.3	13–46		Level to SW-facing; 0°–3° slope
	Sagebrush/ Junegrass	67	1.3	21–62		
91 Colony	Junegrass	63	1.3	15–31		Level to gently sloping; 0°–6° slope
Pickett Creek Colony	Junegrass	74	0.4	15–31		Level to gently sloping S-facing; 0°–2° slope
Thomas Colony	Junegrass	65	1.5	31–46		SE-facing; gentle slope
Lower Bench Colony	Junegrass	73	0.6	31–46		SW-facing; 0°–2° slope
Tonopah Colony	Junegrass	73	1.3	18–62		E-facing; gentle slope
Pump Station Colony	Junegrass	72	1.3	16–62		Level to gently sloping valley
BLM-13 Colony	Junegrass	83	0.4	31–62		Nearly level
Island Colony	Junegrass	71	0.4	15–51		Nearly level
Graveyard Colony	Junegrass	71	0.1	15–62		Nearly level
Timber Creek Colony (Abandoned)	Junegrass	73	0.4	31–51		Nearly level
HISTORIC FERRET HABITAT						
2. Larsen's Ranch Complex	Birdfoot sage/grass	39	2.5	5–31	2042	Level; 0°–10° slope
3. Wasmer Flats Complex	Alkali sagebrush	53	1.3 (live) 0.7 (dead)	5–62	2095	Level to gently sloping
4. Gillies Draw Complex	Gardner saltbush	58	0.8	8–92	1652–1808	Highly dissected; series of parallel draws and ridges
5. Horne Flats Complex					2042	Extensive, level bench
	Wheatgrass-sedge	66	1.1	26–41		
	Mixed shrub/ grass	59	1.7	31–36		
	Gardner saltbush	56	1.6	10–41		

[1]Becker and Alyea, 1964a
[2]Becker and Alyea, 1964b
[3]G = Grazed
PL = Pipeline
PW = Powerline
OW = Oil well
TL = Transmission line

METHODS

Ten of 33 white-tail prairie dog colonies uti-lized by BFF's and an abandoned colony near Meeteetse, Wyoming (Forrest et al. 1985), were arbitrarily selected for study (Table 1). Four historic BFF habitat sites (Larsen's Ranch, Wasmer Flats, Gillies Draw, Horne Flats; Table 1) were selected for comparison with the current BFF habitat site at Mee-teetse. Historic habitat was identified based on the presence of BFF skeletal remains or sign (Martin and Schroeder 1979, 1980, Clark 1980, Clark and Campbell 1981).

All five sites were similarly inventoried. Vegetation type units were delineated on 7.5 minute USGS topographic maps during field reconnaissance and named based on aspect dominance. Sampled types were later re-named for the dominant-co-dominant spe-cies.

Thirty randomly selected plots per vegeta-tion type containing prairie dog burrows were sampled in each of the 11 mapped Meeteetse colonies. Colony boundaries within the four historic BFF habitat sites were not delineated for the authors, and no attempt to do so was

Mean monthly temp. extremes High	(°F)[1] Low	Mean annual precipitation (cm)[2]	Disturbance[3]	Additional vegetation types present not containing burrows
45	21	43.9		Mixed shrub; mixed grass; riparian; greasewood; rabbitbrush; wet meadow
			G; PL; OW; TL	
			G; PL	
			G	
			G	
			G	
			G	
			G	
			G; PL	Wet meadow
			G; PL; PW	
			G	
			G	
			G	
47	7	16.7	G	Sagebrush
43	4	27.0	Sprayed; G	Western wheatgrass playa; sagebrush
45	21	43.9	G; TL	Sagebrush; greasewood
67	21	26.7	G; PL; TL	Sagebrush

made in the field. Rather, vegetation types within the arbitrarily designated study sites were mapped as previously described, and only those types containing burrows were sampled. A minimum 30 plots per vegetation type containing prairie dog burrows was sampled at each of these four complexes, with plots randomly distributed throughout several colonies within each complex. Additional plots were sampled when required to meet sample size adequacy as defined by the Wyoming Department of Environmental Quality (1979). A 0.5 m x 2.0 m frame was used to

delineate plot boundaries. Percent bare ground, litter and rock, and cover by species were determined by ocular estimate. Shrub density was sampled using a 4.0 m x 4.0 m plot located at one corner of the 1 m² plot. Number of stems and height measurements were recorded for each shrub species rooted in this plot.

Floristic inventories were made of all five complexes. Additional qualitative observations, including past and current disturbance, degree and source of disturbance, soils, topography, relative abundance and distribu-

TABLE 3. Summary cover and shrub density data for all five prairie dog complexes.

Prairie dog complex	Cover[1]						Density
	x̄ graminoid	x̄ forb	x̄ shrub	x̄tpc*	x̄ bare	x̄ litter	x̄ shrubs/m²
CURRENT FERRET HABITAT							
1. Meeteetse Complex							
Core Colony							
Sagebrush/							
Junegrass	39.7	16.2	11.0	66.8	18.7	14.8	1.3
Junegrass	48.2	24.1	1.1	73.4	9.7	17.0	0.3
91 Colony	45.0	9.1	9.1	63.1	29.7	7.6	1.3
Pickett Creek Colony	48.7	23.3	1.8	73.7	10.3	15.7	0.4
Thomas Colony	46.0	13.1	6.0	65.1	31.7	5.4	1.5
Lower Bench Colony	42.8	29.9	1.3	74.1	22.0	6.1	0.6
Tonopah Colony	51.6	12.5	8.6	72.7	21.6	6.0	1.3
Pump Station Colony	44.4	18.3	9.7	72.3	25.8	4.9	1.3
BLM-13 Colony	55.7	25.7	1.9	83.3	10.2	9.2	0.4
Island Colony	46.2	21.2	3.4	70.7	21.8	9.9	0.4
Graveyard Colony	47.3	23.7	0	71.0	18.9	11.6	0.1
Junegrass type mean	47.6	20.1	4.3	71.9	20.2	9.3	0.9
Timber Creek Colony (abandoned)	45.5	25.4	2.2	73.1	19.0	10.1	0.4
HISTORIC FERRET HABITAT							
2. Larsen's Ranch Complex	14.4	6.7	17.4	38.5	58.3	5.0	2.5
3. Wasmer Flats Complex	26.0	12.1	14.8	52.9	32.9	16.0	1.3 (live)
4. Gillies Draw Complex	34.3	3.3	20.3	57.8	33.4	9.0	0.7 (dead)
5. Horne Flats Complex							
Grass	45.0	10.9	9.6	65.5	23.6	11.0	1.1
Shrub/Grass	24.1	12.3	22.9	59.4	35.6	5.4	1.7
Saltbush	13.0	17.5	25.9	56.3	39.8	4.3	1.6

[1]Percent aerial cover

*Total plant cover

tion of prairie dog burrows, and community structure, were also recorded.

RESULTS

Current BFF Habitat

MEETEETSE.—This 3887 ha site is located about 10 km northwest of Meeteetse, Wyoming. It is characterized by extensive, gently rolling, grassy benches ranging in elevation from 2134 m to 2256 m. Soils are medium textured, contain less than 50% coarse frag- ments, and are either deep (128–154 cm) or underlain by soft or unconsolidated geologic material (Meyer 1983, personal communica- tion) (Table 2). Primary land use is domestic livestock grazing.

Eight vegetation types occur in the BFF-oc- cupied study site. They are greasewood (*Sar- cobatus vermiculatus*), wet meadow, rabbit- brush (*Chrysothamnus nauseosus*), mixed shrub, riparian, mixed grass, junegrass (*Koe- leria cristata*), and sagebrush/junegrass (*Artemisia tridentata/K. cristata*). Only the- latter two types contain prairie dog burrows.

Ten of the 11 colonies lie entirely within the junegrass type, whereas one, Core Colony, is vegetated by the junegrass and sagebrush/ junegrass types (Tables 2, 3). Mean total plant cover for the BFF-utilized junegrass type ranges from 63 % to 83 % aerial cover, with grasses the dominant species. The BFF-uti- lized sagebrush/junegrass type has a mean to- tal plant cover of 67%, with sagebrush the dominant shrub (Tables 3, 4). Plant heights range from 13 to 62 cm in these two types. The Timber Creek Colony was probably poisoned and abandoned 10 to 20 years ago (Clark 1985, personal communication). Plant cover and shrub density values for the junegrass type in which this colony lies are all within corre- sponding value ranges of the BFF-occupied prairie dog colonies. Species composition and plant heights are also similar (Tables 2, 3, 4). This may indicate that, unlike blacktail prairie dogs (*C. ludovicianus*) (Bonham and Lerwick 1976), white-tails do not significantly alter vegetation of their colony. However, it was not the purpose of this study to determine such effects.

The junegrass-dominated grasslands may be a result of historical heavy grazing by livestock of native bluebunch-western wheatgrass (*Agropyron spicatum-A. smithii*) communities. Historic photographs of the Meeteetse study area at Buffalo Bill Museum in Cody, Wyoming, indicate historic heavy cattle use of the area during various seasons. Changes in species composition similar to those indicated at Meeteetse have been documented in Oregon and Washington (Baker 1983, personal communication).

Historic Ferret Habitat

The four historic BFF habitat sites are discussed separately.

LARSEN'S RANCH.—This 259 ha study site is located about 18 km north of Wamsutter, Wyoming (Table 1). Topography is level to gently sloping uplands with 0° to 10° slope. Mean elevation is about 2042 m (Table 2). Soils are predominantly of the Tresano-Sandbranch, nonalkaline subsoil-Sagecreek complex (Holbrook 1983, personal communication).

Two vegetation types were present, birdfoot sagewort/western wheatgrass and sagebrush (*Artemisia tridentata*). Burrows occurred only in the former, which was characterized by 58% bare ground and 39% total plant cover (Tables 3, 4). Dominant species are those for which the type was named. Plant heights range up to 31 cm.

The area appeared highly disturbed by cattle at the time of sampling. It was trampled and vegetation was often grazed to within 6 cm of the soil. Not far from where a BFF skull was found were an abandoned barn and corral, water troughs, and salt licks around which cattle congregate. The resulting disturbance, however, did not appear to limit prairie dog use of the area.

WASMER FLATS.—This site is located in a north-south trending valley approximately 24 km northwest of Evanston, Wyoming (Table 1). It encompasses about 6323 ha and is characterized by gently to moderately sloping topography (Table 2). Elevation is about 2095 m. Soils are characteristically very shallow to deep sandy, clayey, gravelly, cobbly, saline-alkaline soils on sandstone, shale, tuff, and conglomerate (United States Department of Agriculture Soil Conservation Service 1981). Primary land use is rangeland.

The site is predominantly a complex mosaic of vegetation in which no single species clearly dominates (based on cover). Alkali sagebrush is the shrub with the greatest density (Tables 2, 3) and provides the type with its overall aspect. Total plant cover is 53% (Table 3), with grasses providing nearly half this value. Species providing the most cover include bottlebrush squirreltail (*Sitanion hystrix*), western wheatgrass, Sandberg bluegrass (*Poa secunda*), and alkali sagebrush (Table 4). Plant heights range from 5 to 62 cm. Prairie dog burrows are scattered along the valley bottom and on lower slopes where shrubs occur as scattered individuals or in small clumps. They do not occur in areas that appear to be periodically flooded, such as the western wheatgrass playa at the north end of the study site or in taller vegetation, such as the alkali sagebrush stands on upper slopes and the sagebrush (*Artemisia tridentata*) community at the northern end of the study site.

The entire valley has been sprayed, as is evidenced by the high density of dead alkali sagebrush sampled (Table 4). Spraying appears to have been most successful along the valley bottom and lower slopes, where the greatest number of dead shrubs and lowest live shrub densities were observed. The site is also crossed by several dirt roads and is paralleled by a major highway. These roads allow easy access by humans, who were twice observed shooting prairie dogs from the roadside during the sampling.

GILLIES DRAW.—This site is located approximately 40 km southeast of Meeteetse, Wyoming (Table 1). It is an area of highly dissected topography, characterized by a series of nearly parallel ridges separated by steep-sided valleys. Elevation ranges from 1652 to 1808 m (Table 2). The approximately 12,646 ha study site generally includes Gillies Draw itself and adjacent ridges on the east and west. Soils are typically Cadoma, Cushman, and Ulm soil types (Meyer 1983, personal communication). Primary land use is domestic cattle and sheep grazing.

Vegetation forms a complex pattern. The valley bottom, lower slopes, and isolated level areas support a Gardner saltbush/mixed grass vegetation type. Sagebrush (*Artemisia tridentata*) dominates side-slopes and ridges and

TABLE 4. Dominant plant species[1] sampled in each of the five prairie dog complexes.

Species	Core[4]	91	Pickett Creek	Thomas	Lower Bench	Tonopah	Pump Station	BLM 13	Island
					Meeteetse Complex[2]				
GRASSES									
Agropyron dasystachyum	7, 8		12	6	4	5	10	4	12
Agropyron smithii					5				
Agropyron spicatum		6		8					
Agropyron trachycaulum									
Bouteloua gracilis									
Bromus tectorum									
Carex filifolia						8		4	
Koeleria cristata	10, 21	18	16	13	10	13	11	18	7
Oryzopsis hymenoides									
Poa secunda	6, 11	8	9	6	6	17	18	10	19
Sitanion hystrix									
Stipa comata	4, 0	6	5		15	6		19	5
FORBS									
Artemisia frigida	6, 12	4	11	3	8	4	6	4	7
Astragalus adsurgens					3			3	
Astragalus grayi		2		3			2		
Astragalus spatulatus									
Descurainia pinnata									
Oxytropus deflexa	0, 3		3		3			4	3
Phlox hoodii	4, 4	2	4	3	5	2	3	8	5
Ranunculus testiculatus									
Sphaeralcea coccinea			2						
Vicia americana							2		4
SHRUBS									
Artemisia longiloba									
Artemisia petadifida									
Artemisia tridentata	9, 0	3							
Atriplex gardneri		2		2		6	6		
Chrysothamnus nauseosus	0, 3		1					1	
Chrysothamnus viscidiflorus									
Eurotia lanata		3		2					
Gutierrezia sarothrae	0, .3			2	1			1	
Opuntia polyacantha	0, .3		1						

[1]Dominance based on cover; only dominant species listed.
[2]Current BFF habitat.
[3]Historic BFF habitat.
[4]Value listed first is for *A. tridentata*/*K. cristata* vegetation type; value listed second is for *K. cristata* vegetation type.

also occurs as stringers along drainages and as small inclusions within the saltbush type. Greasewood (*Sarcobatus vermiculatus*) forms dense stands primarily along the main drainage. Prairie dogs utilize only the salt bush type, where plant heights range from 8 to 92 cm. Total plant cover is 58% (Table 3). Dominant species are Gardner saltbush and a mixture of grasses (Table 4).

HORNE FLATS.—This site is approximately 7 km south of Medicine Bow, Wyoming (Table 1) at an elevation of 2088 m (Table 2). It is an extensive flat bench whose topography and aspect are very similar to those of the Mee teetse study site. Soils have not been mapped.

The study site encompasses about 14,227 ha, although similar habitat and prairie dog colonies are extremely extensive outside the study site boundaries as well. Primary land use is livestock grazing, and areas near water troughs and salt licks are most heavily im pacted.

Four vegetation types, thickspike wheat grass-threadleaf sedge (*Agropyron dasys tachyum-Carex filifolia*), mixed shrub/mixed grass, Gardner saltbush, and sagebrush (*Artemisia tridentata*) occur in the study site. Prairie dogs utilize the former three types. Burrows are evenly spaced in the grass type. They are unevenly distributed in the two

Graveyard	Timber Creek	Junegrass Average	Larsen's Ranch Complex[3]	Wasmer Flats Complex[3]	Gillies Draw Complex[3]	Horne Flats Complex[3]		
						Grass-Sedge	Shrub/Grass	Salt bush
10		7						
		1	11	7	4	11	9	6
	8	2						3
				5				
						4	8	
					5			
		3				17		
16	19	13				3		
		.3			3			
10	10	12	4	7	8			
				8				
7	5	7				7		
10	7	7					4	
4	2	1						
		1						
						3		
				2	2			
3	6	2						
	5	4	6	5		6	5	14
				4				
		1						
		1						
				6				
			14		6	7	9	9
		.3					7	
		2	3	3	14			14
		1						
				3				
		1						
	1	1					3	
		.2						

shrub types and appear to be most dense in the Gardner saltbush type.

The thickspike wheatgrass-threadleaf sedge type is the most extensive type in the study site. Total plant cover (Table 3) is 66%, most of which is provided by graminoid species. Plant heights range from 26 to 41 cm. Broom snakeweed (*Chrysothamnus viscidiflorus*) is the predominant shrub. The second most extensive vegetation type is the mixed shrub/mixed grass type, characterized by vegetation 31 to 36 cm tall. Birdfoot sagewort, thickspike wheatgrass, blue grama (*Bouteloua gracilis*), and sagebrush are the predominant species. Total plant cover is 60% (Table 3), with grasses

and shrubs contributing nearly equal cover (Table 4). The Gardner saltbush type occurs in small depressions. Total plant cover is 56%, nearly half of which is provided by shrubs (Table 3). Important species include Hood's phlox (*Phlox hoodii*) and birdfoot sagewort. Plant heights do not exceed 41 cm.

DISCUSSION

Comparisons of measurements and qualitative observations reveal similarities among the five study sites.

1. *Vegetation*. At all five sites, vegetation types in which prairie dog burrows occur are

generally characterized by vegetation of low stature (< 92 cm). This figure represents the tallest plants observed, which usually occur as scattered individuals or clumps. Overall as pect of these vegetation types is one of shorter plants. At the Meeteetse site (current BFF habitat), maximum plant height is 62 cm. The tallest plants are represented by scattered sagebrush or isolated patches of species such as needle and thread (*Stipa comata*), green needlegrass (*S. viridula*), Sandberg bluegrass (*Poa secunda*), and tansymustard (*Descur-ainia pinnata*). Vegetation of the historic BFF habitat sites is generally shorter than that of the Meeteetse site. The tallest plants ob served were scattered tansymustard (92 cm) in Gillies Draw. At all sites mat-forming shrubs, such as birdfoot sagewort and Gard-ner saltbush, do not exceed 26 cm. Where inclusions of tall shrubs occur, prairie dog burrows are located only on their peripheries.

2. *Burrow Distribution*. When a prairie dog colony lies entirely within one extensive vege tation type, such as 10 of the Meeteetse colonies do, burrows are widely distributed and are about equidistant from one another. When two or more vegetation types occur as a mosaic and only one type is suitable prairie dog habitat, such as at Gillies Draw and Larsen's Ranch, burrows are closer together and distances between them vary. Similar patterns in burrow distribution were ob served at all five study sites.

3. *Topography*. All prairie dog colonies sampled occur on level to moderately sloping sites with various exposures. When steep slopes occur, prairie dog burrows are located only in valley bottoms and on lower side slopes, even if a suitable vegetation type fol lows the steeper slope. This is exemplified best at Gillies Draw, where the Gardner salt bush type occurs over a variety of slopes but contains burrows only where the topography is level or moderately sloping. At Meeteetse a few small, isolated hills exist that support the junegrass vegetation type and are surrounded by burrows at their bases, but burrows are absent from the slopes.

4. *Disturbance*. All sites were disturbed by human-related activities. The Meeteetse site has been variously grazed by domestic live stock for over 100 years. It is crossed by pipe lines, transmission lines, fences, and roads. It supports several oil wells and associated struc tures, corrals, salt licks, and other ranch struc tures. The four historic BFF habitat sites have been similarly disturbed. As they all occur on public lands, are relatively accessible, and are presently grazed, it is not unreasonable to assume that they, too, have been used as cat tle and sheep rangeland for many years. All are crossed by one or more of the previously mentioned man-made structures. The Larsen's Ranch site is located in a large, active oil and gas field. In addition, the entire valley in which Wasmer Flats is located was sprayed, presumably to reduce shrub cover and in crease grass cover several years ago. The site is also easily accessible to humans, who were twice observed by the authors to stop and shoot at prairie dogs from the roadside.

In conclusion, it is obvious that white-tail prairie dogs are not dependent upon a partic ular vegetation type to meet habitat require ments. They appear to survive equally well in grass, shrub, or shrub/grass types where pre dominant plant heights do not exceed about 62 cm. They also appear to be extremely toler ant of high degrees of disturbance for long periods of time. Consequently vegetation cannot be considered an important parameter in identifying suitable BFF habitat.

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COMPARISON OF CAPTURE-RECAPTURE AND VISUAL COUNT INDICES OF PRAIRIE DOG DENSITIES IN BLACK-FOOTED FERRET HABITAT

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ABSTRACT.—Black-footed ferrets (*Mustela nigripes*) are dependent on prairie dogs (*Cynomys* spp.) for food and on their burrows for shelter and rearing young. A stable prairie dog population may therefore be the most important factor determining the survival of ferrets. A rapid method of determining prairie dog density would be useful for assessing prairie dog density in colonies currently occupied by ferrets and for selecting prairie dog colonies in other areas for ferret translocation. This study showed that visual counts can provide a rapid density estimate. Visual counts of white-tailed prairie dogs (*Cynomys leucurus*) were significantly correlated ($r = 0.95$) with mark-recapture population density estimates on two study areas near Meeteetse, Wyoming. Suggestions are given for use of visual counts.

Recovery of the endangered black-footed ferret will involve the careful management of the only known population near Meeteetse, Wyoming, as well as captive breeding and translocation. Both ferret preservation and population recovery are dependent on the presence of prairie dog colonies. Ferrets have been most frequently observed in or near prairie dog colonies (Cahalane 1954, Henderson et al. 1969), and their original distribution probably corresponded closely to the range of the black-tailed (*Cynomys ludovicianus*) and white-tailed prairie dogs (Hall 1981). The black-footed ferret relies on the prairie dog for approximately 90% of its diet (Henderson et al. 1969, T. M. Campbell personal communication) and on prairie dog burrows for shelter and rearing young. Prairie dog populations declined dramatically during the last century because of loss of habitat and poisoning. From an estimated 283 million ha occupied in the late 1800s (Merriam 1902), prairie dog colonies declined to less than 0.6 million ha by 1971 (Cain et al. 1971). The decline of the black-footed ferret during the last century is probably linked to the reduction in prairie dog populations.

A model using growth rates of Siberian polecats to simulate those of black-footed ferrets estimated the annual prey requirement of the black-footed ferret to be 214 black-tailed prairie dogs (Stromberg et al. 1983) . They assumed an intrinsic rate of growth of 1.5 for prairie dog populations and calculated the prairie dog population size required to support a ferret at 766. Because white-tailed prairie dogs are larger, their model predicted the annual prey requirement to be 186 animals and the required population size to be 666. In telemetric studies, a radio-tagged black-footed ferret preferred areas of dense prairie dog burrows within its home range (Biggins et al. 1985), and we postulate that high prairie dog densities are important to ferrets.

A rapid method of determining prairie dog population density needs to be developed that can be used to assess the prairie dog populations at Meeteetse and that would allow us to monitor prairie dog populations at frequent intervals for potential problems, such as plague outbreaks or effects of oil development. A rapid density estimation procedure also could be used to assess prairie dog populations in colonies being considered for ferret translocation.

Prairie dog population numbers have been estimated using a variety of methods. Mark-recapture is a reliable method for estimating the density of prairie dogs because these animals have relatively small home ranges and are readily trapped. However, mark-recapture is labor intensive and can be done only on relatively few plots; it is therefore impractical for estimating animal density over large areas. Closing burrows and counting the number

reopened after 1 or 2 days is a method fre- quently used in conjunction with control pro- grams, where pretreatment and posttreat- ment counts are compared to determine the effectiveness of rodenticide applications to prairie dog populations (Tietjen 1976). The method provides an index to prairie dog activ- ity that may have little correlation with actual population trends (Knowles 1982); results can be variable with this technique because one prairie dog can reopen more than one burrow.

Visual counts may provide a quick method of measuring prairie dog density; prairie dogs are well suited for visual counts because of their large size, their diurnal activity patterns, and their tendency to live in social colonies. Visual counts were used by Knowles (1982) to estimate black-tailed prairie dog numbers, but their precision was not assessed for white- tailed prairie dogs. This study evaluated the use of visual counts to monitor white-tailed prairie dog densities by comparing visual counts with mark-recapture data.

Study Area

The study was conducted 30 km southwest of Meeteetse, in Park County, Wyoming. White-tailed prairie dogs occur in colonies on about 3000 ha (Clark et al. 1984) throughout this area. We studied two colonies located between 2280 and 2380 m in elevation on short- to midgrass rangeland.

Methods

Mark-Recapture

Prairie dog populations were censused by mark-recapture during May and July 1984 and May 1985. A 360 x 360 m trapping grid was established on each of the two study colonies using 169 National[3] live traps (48 x 15 x 15 cm) located at 30 m intervals. The grid was subdi- vided into nine 120 x 120 m subplots. Before each trapping period, the traps were wired open and baited with flaked oats for a two-day familiarization period. During the subse- quent five-day trapping period, the traps were baited with oats and checked during the morning; they were closed at midday to avoid prairie dog mortality caused by heat stress. The trapped prairie dogs were aged (juvenile or adult), sexed, ear-tagged with monel No. 1

fingerling fish tags, and released at the point of capture. Population estimates for each of the trapping periods were computed using the computer program CAPTURE (White et al. 1978). Otis et al. (1978) have provided a detailed reference on the theory behind pro- gram CAPTURE.

Visual Counts

Prairie dogs on the study area were ob- served prior to the initiation of this study. They exhibited a bimodal activity pattern with peak numbers aboveground between 0700 and 1000 hours and with a second but lower peak between 1500 and 1800 hours. This bi- modal activity pattern is similar to that ob- served by Tileston and Lechleitner (1966) and Clark (1977) for white-tailed prairie dogs and by Althen (1975) for black-tailed prairie dogs. Visual counts were therefore conducted dur- ing the peak activity period in the morning on four consecutive days following the trapping period. During May 1984 prairie dogs were counted from portable 3–m-high towers erected in the center of each 120 x 120 m subplot. Counts from the center of each sub- plot proved labor intensive, so during July 1984 and May 1985 prairie dogs were counted from two locations outside the entire 360 x 360 m grid; observers were located a minimum of 30 m from the grid to minimize disturbance of animals. Two observers counted the grid from each location. Prairie dogs on each 120 x 120 m plot were counted during a four-minute period by scanning the plot with binoculars and a 15X spotting scope. Three counts were made daily of each plot during a two or three- hour period. Plots were counted in the same sequence and at synchronized times by ob- servers at both locations. Prairie dogs that were located on the borders between two plots were counted if they were on the north and east edges and not counted if on the south and west edges.

Statistics

Simple linear correlation coefficients were computed (1) between the highest total count of individual prairie dogs over the entire 360 x 360 m grid and the population density gener- ated by program CAPTURE for the corre- sponding five-day period and (2) between the highest single count of individual prairie dogs
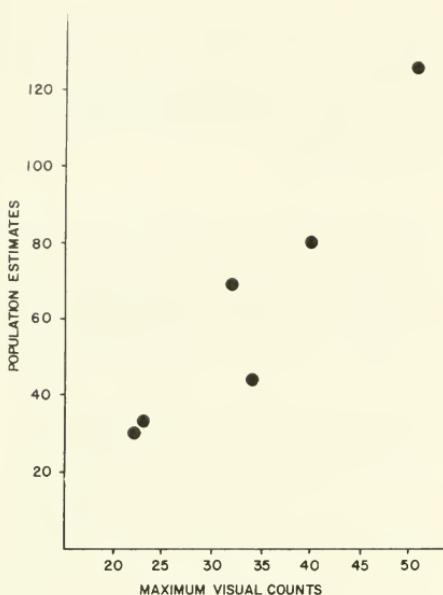
Fig. 1. Prairie dog population estimates on 360 by 360 m grids (x-axis) plotted against maximum visual counts on the same areas (y-axis). The simple linear regression equation is: y = 15.56 + 0.28x.

per 120 x 120 m plot and the number of prairie dogs trapped on that plot during the corre- sponding five-day trapping period (insuffi- cient numbers of prairie dogs were trapped on each 120 x 120 m plot to generate a satisfactory population density).

The variation associated with location, ob- server, day, and trial (three counts per day) was determined using a procedure on SAS (SAS 1985) that estimates variance compo- nents (PROC VARCOMP).

Results

There was a high correlation between the population densities estimated by CAPTURE and the highest number of animals counted visually across the entire 360 x 360 m grid during the corresponding period ($r = 0.95$, P = 0.004, Fig. 1). The simple linear regression equation is: y = 15.56 + 0.28x, where y is the maximum visual count and x is the population density. Population density correlated better with visual counts than the total number of

animals trapped ($r = 0.84$). Also, the maxi- mum number counted provided a better cor- relation than the average of a series of counts ($r = 0.74$).

There was a lower correlation between the highest count and number trapped per 120 x 120 m sub-plot ($r = 0.69$); when analyzed separately by time period the correlation was highest during May 1984 ($r = 0.86$) and lower during July 1984 and May 1985 ($r = 0.70$ and 0.61, respectively). Visual counts on small ar- eas may therefore not be as representative of actual densities as counts on larger areas.

Variance component estimation revealed that trials (counts per day) accounted for the most variation in the data (Table 1). This was expected because counts were begun in the morning as prairie dogs emerged from bur- rows and were continued until prairie dogs became less active above ground in midmorn- ing. During any day, counts were normally low at first, increased to the maximum count, then decreased. Location accounted for a large portion of the variation in the data on area 1 but only a small portion of the variation on area 2. Location was important on study area 1 because tall grass grew on a portion of the study area between the time the area was chosen and the time when visual counts were begun. The grass made counting prairie dogs on part of the plot difficult from one of the two locations.

When trials were removed from the analysis and only the maximum count by each ob- server per day was used, location still ac- counted for a large portion of the variation in the data on area 1. Day variation was small for area 1 (only one-third of location variation) but was comparatively large for area 2. Observer variation was negligible, but a large variance component existed for observer-day interac- tion. This would indicate that variability was present between observers over the four-day period but that observers had no consistent bias toward high or low counts.

Discussion

Visual counts appear to provide a useful in- dex to prairie dog population densities that can be used to monitor prairie dog popula- tions at Meeteetse and to assess ferret reloca- tion sites. Mark-recapture is a reliable

TABLE 1. Components of variance for prairie dog visual counts of two study areas near Meeteetse, Wyoming. On each study area, counts were conducted over a four-day period from two locations by two observers at each location. The magnitude of the variance indicates the relative influence of each item in the model to the overall variation.

Source	df	Area 1	Area 2	Area 1[1] maximum count	Area 2[1] maximum count
Location (L)	1	11.34	−1.54[2]	20.77	−2.64
Observer (0) in L	2	2.73	−0.44	−0.54	−3.17
Day (D)	3	−1.49	3.60	6.70	13.92
D x L	3	21.75	4.81	−15.94	−3.58
O x D in L	6	−4.38	−2.41	44.62	14.67
Trial in O x D	32	33.96	23.77		

[1]Trials were removed from this analysis, the maximum count per observer per day was analyzed.

[2]Negative variances are usually considered to be zero.

method for estimating the abundance of white-tailed prairie dogs because these animals are readily trapped and have relatively small home ranges. The estimates of density using mark-recapture and visual counts were independent of one another in this study and produced comparable results. Therefore, unless both methods were equally biased, the accuracy of visual counts was probably good. Knowles (1982) found that visual counts of black-tailed prairie dogs provided a good correlation between maximum counts and population levels ($r = 0.942$).

Size of areas counted influences the reliability of visual counts. Visual counts on small areas of 1 to 1.5 ha did not correlate as well with numbers of animals trapped on those areas because of the increased edge effect on the smaller areas or because prairie dog home ranges exceeded the area counted and movement occurred between areas of locally high and low densities. Size of areas counted should therefore be 10 ha or greater if possible.

Because maximum counts provided better correlations with prairie dog population densities than the mean of a series of counts, counts should be made during peak activity periods in early morning or late afternoon. Trials (counts per day) accounted for the most variation in the data because counts were made from the time prairie dogs emerged early in the morning until they disappeared as temperatures increased. Because of this variation, it is important that visual counts be made over a two- or three-hour period during peak prairie dog activity so a count of maximum numbers above ground is included. Because prairie dog activity is suppressed by high and

low temperatures (e.g., below 10 C or above 27 C) and strong winds (Davis 1966, Althen 1974), counts should be conducted when weather conditions are moderate.

Seasonal variation also exists in the percentage of prairie dogs active above ground (Tileston and Lechleitner 1966, Clark 1977). Individual prairie dogs are active for only four to five months during the year. Adults emerge from hibernation in early spring and become inactive in midsummer, whereas juveniles appear above ground in early June and remain active until late October or November. The total population therefore attains its maximum size during late June and early July when adults and juveniles are above ground at the same time. Surveys during this period would therefore most accurately reflect total population levels.

Substantial variation occurred among locations when observers at one of the locations on area 1 were not able to see portions of the plot well because of intervening tall grass. Locations of observers for conducting counts should therefore be chosen carefully so the entire area to be counted is readily visible. In areas of flat topography the roof of a vehicle provided a good location from which to make visual counts.

The variance component for days was small for area 1, indicating that counts made on one day might be sufficient. However, the variance component was larger for area 2. A zero variance component existed for observers in this study, indicating that different individuals could count on different days and an accurate estimate of population density could still be obtained. However, because a large component was associated with observer-day in-

teraction and because a large day component was present on one area, we recommend that counts be made over several days by the same observer.

Although visual counts can be a precise method of estimating prairie dog populations, they should be used with caution. Precision is based upon their repeatability. Therefore, the observer, location, and time of day should remain constant between one count and the next whenever possible. The area to be counted should be predetermined and its boundaries well marked so that prairie dogs outside the area will not be counted. Systematic scans of an area for predetermined time periods can minimize the possibility of counting animals more than once; the only animals counted twice are those that move across the study area during the scan. If conducted following the guidelines suggested, visual counts can be a valuable technique for estimating prairie dog densities.

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HABITAT SUITABILITY INDEX MODEL FOR THE BLACK-FOOTED FERRET: A METHOD TO LOCATE TRANSPLANT SITES

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ABSTRACT.—A Habitat Suitability Index Model (HSI), following the U.S. Fish and Wildlife Service HSI Model Series, is described for the black-footed ferret. The literature on which the model is based is reviewed, and model assumptions and structure are discussed. A realistic model is specified with variables and their functions that embody the critical spatial and resource heterogeneity characteristic of the broad geographic environment ferrets occupy. It assumes that ferrets can meet year-round habitat requirements within prairie dog colonies providing: (1) prairie dog colonies are large enough, (2) burrows are numerous enough, and (3) adequate numbers of prairie dogs and alternate prey are available. Five habitat variables are identified: V1 is the frequency distribution of colony sizes, V2 is the total area of colonies, V3 is burrow opening density, V4 is intercolony distance, and V5 is prairie dog density. Variables are compensatory. As more data become available and our understanding of ferrets expands, the basic model design can readily incorporate improvements without radical restructuring.

Habitat models are an attempt to describe and quantify an animal's essential habitat require ments or "life requisites" and are therefore a useful tool in habitat evaluation. The Habitat Suitability Index (HSI) Model Series, developed by the U. S. Fish and Wildlife Service (USFWS), provides habitat descriptions for several species. These models are useful for assessment of im pacts on wildlife and habitat management (US FWS 1980a, b) and may prove especially valu able in endangered species management, where determination of habitat quality and suitability is often critical for management and continuation of the species. HSI "models should be viewed as hypotheses of species-habitat relationships ra ther than statements of proven cause and effect relationships" (Schamberger et al. 1982:1).

This paper applies the HSI Model format to the Meeteetse, Wyoming environment of the black-footed ferret (*Mustela nigripes*; BFF) as generally described by Clark et al. (*Description and history*, 1986) and more specifically by Forrest et al. (1985)(Fig. 1). Applications and uses of the model are: (1) to compare other areas to BFF habitat at Meeteetse, (2) to use those comparisons to select areas to be searched for BFFs, and (3) to select suitable areas for transplant sites. Our use of the HSI format closely follows the USFWS (1981) and parallels applications by Allen (1982a, b, 1983, 1984) for other species.

Our use of the HSI model for BFFs incorpo rates several recent improvements on the roles of ecological models: (1) We stress model reality of a single species more than focus upon model precision or generality (see Levins 1966, Rosen 1978, Kaiser 1979, Pielou 1981). (2) Few highly measurable variables dictate the HSI, and, although some are colin ear, together they contain high explanatory power, at the same time allowing comprehen sible results and simplified sensitivity analy sis. This reflects the growing consensus that there is no apparent relation between model complexity and predictive utility in any field of forecasting (e.g., Ascher 1978, K. E. F. Watt personal communication). (3) Our model uses nonlinear representations of variables, rather than linear, because those more accu rately express the dynamic nature of biologi cal responses and realistic species-habitat re lations (Whittaker 1975, Green 1979, West man 1980, Johnson 1981, Meents et al. 1983) . Nonlinearity permits us to mimic more realis tic biological processes that involve thresh olds and limits and the smoothed transitions between them (Holling 1985, J. R. Krebs per sonal communication). (4) The model vari ables and their functions embody the critical

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Fig. 1. Photographs of black-footed ferret habitat (prairie dog colonies and prairie dogs) and ferret predation. Photos by Tim Clark.

A. White-tailed prairie dog colony occupied by ferrets.

B. Black-footed ferret at prairie dog burrow.

C. Two white-tailed prairie dogs.

D. Black-footed ferret with prairie dog prey.

importance of spatial and resource heterogeneity. The structural simplicity of the BFF-prairie dog (*Cynomys* spp.) community promotes a design where all variables directly assess spatial patchiness and resource variability, considerations that have pivotal impact on population dynamics and population viability (reviews in Steele 1974, Wiens 1974, Southwood 1977, Shugart 1981).

The outcome of the above four features is only a slight increase in model complexity traded for a dramatic increase in ecological reality. Perhaps of equal benefit is the ease of model validation. As more data become available and our understanding of BFFs expands, the basic model design can readily incorporate improvements without radical restructuring. Data sets already completed and cited below could likely be reevaluated with future model versions.

This HSI application for the BFF draws on Clark et al. (*Description and history*, 1986) and Forrest et al. (1985), who describe the Meeteetse, Wyoming, BFF study area (1981–1985) and its use by BFFs as well as all the data from the Mellette County, South Dakota, BFF study (1964–1974). Because of the localized nature and limited size of these two study areas, this HSI model will likely require updating if BFFs are found in other areas in different ecological settings. In the meantime, this HSI model can serve as a useful tool in BFF recovery planning to evaluate proposed transplant/relocation sites.

BACKGROUND

Requests for evaluation of BFF habitat have been frequently mentioned in the literature. The Black-footed Ferret Recovery Team (1978) requested research to define components of a prairie dog colony necessary to support BFFs. The BFF Recovery Plan also notes the need to establish ideal habitat sites for successful introduction of transplanted BFFs (see Linder et al. 1972) . The South Dakota BFF and Prairie Dog Workshop in 1973 suggested several BFF management needs, in cluding a definition of habitat (Hillman and Linder 1973, Stuart 1973, Erickson 1973). Others have discussed the need for BFF preserves and habitat descriptions (Clark 1976, 1984, 1986). Flath and Clark (1986) described historic prairie dog distributions in Montana

for the period 1908–1914. This early Montana situation probably represented a habitat setting in which BFFs evolved among the complex interrelationships of species and environmental interactions of the prairie dog ecosystem.

Hillman et al. (1979) described prairie dog distribution in the area occupied by BFFs in South Dakota. Their description was widely used by management agencies as a guide to the number and spacing of prairie dog colonies to be left after prairie dog eradication programs.

Clark et al. (*Description and history*, 1986) provided a descriptive and historical overview of the Meeteetse BFF environment. Forrest et al. (1985) noted that BFFs are restricted to a prairie dog complex—a group of prairie dog colonies distributed so that individual BFFs can migrate among them commonly and frequently. The 37 colonies of the Meeteetse complex (total size 2995 ha) were described and their occupation history by BFFs noted. The average density of adult BFFs was 1 BFF/56.6 ha. Burrow openings, based on literature reviews, are correlated with the number of prairie dogs present ($r = 0.71$). High burrow densities are desirable for BFFs in that they provide added protection from predators and shelter from the elements. Colonies greater than 100 ha supported more than two resident adult BFFs, whereas colonies from 12.5 ha to 102.0 ha supported only one BFF throughout the year. BFFs traveled among the colonies, but to an unknown extent. BFFs may use burrows at low densities and colonies of small size in travels between larger colonies. BFFs moving between colonies have a greater chance of finding another colony if the colonies are large and close together.

Several bibliographies of BFFs (Harvey 1970, Snow 1972, Hillman and Clark 1980, Casey et al. 1986) and of prairie dogs (Clark 1971, in preparation, Hassien 1973) exist. These also serve as background for this HSI model. General information on BFFs is summarized in the bibliographies listed above, in primary sources from South Dakota studies (e.g., Hillman 1968, Henderson et al. 1969, Fortenbery 1972), and, more recently, from Meeteetse, Wyoming (e.g., Clark et al., *Description and history*, 1986; Clark et al., *Descriptive ethology*, 1986; Campbell et al. 1985; Richardson et al. 1985; Forrest et al. 1985; Biggins et al. 1985).

Habitat Use Information

Overview

A member of the family Mustelidae, the BFF is the only ferret native to North America (Hall 1981) and is perhaps the rarest and most endangered mammal species on this conti nent (Cahalane 1954, Hillman and Clark 1980). BFFs are solitary except during breed ing and maternal care of young and are pri marily nocturnal. They prey on prairie dogs, whose burrows they also use for cover and litter rearing.

Food

The BFF relies on prairie dogs as its primary food source, although other prey, both live and dead, are taken in considerably lesser amounts (Hillman 1968, Henderson et al. 1969, Sheets and Linder 1969, Sheets et al. 1972, Clark et al. 1985). Sheets et al. (1972) found 91% of 82 BFF scats from South Dakota contained prairie dog remains, and Campbell et al. (unpublished data) found 87% of 86 BFF scats from Meeteetse contained prairie dog remains. Prairie dogs, on this basis, compose the major BFF food.

Stromberg et al. (1983) generated a preda tor-prey model of metabolizable energy re quirements that estimated: (1) annual prey requirements for one reproductive female BFF and her litter of four and (2) prairie dog population sizes needed per BFF. Powell et al. (in press) estimated BFF winter energy expenditure (about 104 kcal/day) and prey re quirements (about 20 prairie dogs from De cember through March) at Meeteetse. A lac tating female with four young are predicted to need six times the winter estimate, or about one prairie dog per day in summer.

Water

BFFs apparently satisfy water requirements through prey consumption and have never been observed in the wild drinking free wa ter. Henderson et al. (1969) reported that captive BFFs drank water irregularly. L. Richardson (unpublished data) watched a BFF eating snow at Meeteetse.

Cover

Cover for BFFs is provided by prairie dog burrows, which are used for predator avoid ance and thermal cover throughout the year (Clark et al. 1985, Richardson et al. in press) Any prairie dog burrow is assumed to be suffi cient to satisfy BFF cover requirements. Higher burrow densities provide greater cover.

Reproduction

Reproductive habitat requirements for BFFs are assumed to be identical to food and cover requirements described above because all BFF activities are associated with prairie dog burrow systems (Clark et al. *Descriptive ethology*, 1986; Richardson et al. in press; Forrest et al. 1985) . Large, mounded, multi entranced burrows may be important for litter rearing because of their presumed extensive tunnel network.

Interspersion

A picture of BFF home range patterns is emerging from research efforts at Meeteetse. A single adult male's range may encompass home ranges of several females, which show much smaller ranges (Richardson et al. un published data). Females remain with their litters until late summer, when young become independent (Henderson et al. 1969, Clark et al. *Descriptive ethology*, 1986). BFFs appear to have a typical mustelid spacing pattern de scribed by Powell (1979), Forrest et al. (1985), and Richardson et al. (in press). More infor mation is needed on BFF home ranges and movements, dispersal of young or adults, and inter- and intrasexual interactions.

Interspersion characteristics of BFFs repre sent a two-dimensional management consid eration—individual and populational. Indi vidual interspersion patterns are better known than populational interspersion pat terns required for minimum population sizes. A resident female snow-tracked from Decem ber through March used 16.0 ha and was over lapped by a resident male that used 136.6 ha (Forrest et al. 1985). Studies of radio-collared BFFs show a young female used 12.6 ha in October and November (Biggins et al. 1985). Population interspersion is dependent on the size, configuration, and intercolony distance of prairie dog colonies making up the com plex. Data show that, if colonies are too small and intercolony distances are too large, then BFF populations cannot sustain themselves.

The search for food (energetics) becomes pro-hibitive, avoidance of predators becomes difficult or impossible, and adequate thermal cover is rare or nonexistent, all reducing both individual and population survival.

Special Considerations

Successful management of BFFs depends on maintaining adequate numbers and areas of prairie dog colonies. Minimum viable population (MVP) sizes and area requirements for BFFs were addressed by Groves and Clark (1986). Additional estimates of these variables are underway by Shaffer et al. (in preparation), who are modeling effects of both demographic and environmental stochasticty on BFF populations of varying sizes. The MVP represents a threshold below which populations are not self-sustaining. Populations may persist for a long time below the MVP, but probably at a loss of adaptability and a high susceptibility to local extinction. Groves and Clark (1986) noted that the genetic method of determining MVP for the Meeteetse BFFs estimated that about 200 animals are needed for maintenance of short-term fitness. The estimated 200 animals needed is about four times the number of breeding adults estimated to currently exist at Meeteetse (Clark 1986).

Poisoning and shooting of prairie dogs should be prohibited from areas where BFFs occur as well as from other selected portions of prairie dog range. Hubbard and Schmitt (1984) suggested a "refugia" concept of managing prairie dogs in which relatively large areas are omitted from poisoning and other disturbance. They suggested that refugia be large enough to support a BFF MVP and based such area estimates on the Stromberg et al. (1983) predator-prey model. Clark (1986) outlined a series of management guidelines for BFFs.

Differences in black-tailed (*C. ludovicianus*) and white-tailed prairie dog colonies have been noted (Tileston and Lechleitner 1966, Campbell and Clark 1981, Clark et al. 1982). Black-tailed colonies often show greater prairie dog and burrow opening densities—two important variables of BFF habitat. Satisfying habitat requirements for BFFs on white-tailed colonies as described in our HSI model is assumed also to satisfy habitat re-quirements on black-tailed and Gunnison's (*C. gunnisoni*) prairie dog colonies.

APPLICATION OF HABITAT SUITABILITY MODEL

Model Applicability

Geographic area. —Although this model was developed on data from the only two BFF populations ever studied, it should apply throughout the historic range of the BFF until additional BFF populations in different ecological settings are found, studied, and results show it does not apply. Even though a single prairie dog colony cannot support a BFF MVP (unless it is extremely large), it can potentially support one or more individuals. Therefore, any prairie dog colony should be considered potential BFF habitat. Historic and current land use patterns affect the quality of BFF habitat. A constellation of prairie dog colonies, described by Clark et al. (*Description and history*, 1986) and Forrest et al. (1985) as a prairie dog "complex," is needed to support a BFF MVP.

Season. —This model has been developed to compare year-round BFF habitat at Meeteetse to habitat in other areas. Because prairie dogs may become torpid or hibernate over winter at northern latitudes, it is recommended that evaluation take place when prairie dogs are active and when snow cover is minimal or absent: late May to late June is recommended.

Cover Types. —This model compares the BFF habitat at Meeteetse to other potential BFF habitat in all cover types where prairie dogs are found.

Minimum Habitat Area. —Minimum habitat area, as discussed for BFFs by Forrest et al. (1985), is defined as the amount of contiguous habitat that is required before an area will be occupied by a species (Allen 1982a). We recommend that a preliminary estimate of 4,000–6,000 ha of prairie dogs is needed to support a MVP of 100 BFFs (Forrest et al. 1985, Groves and Clark 1986).

Model Review. —Drafts of this model were reviewed by our colleagues in the Idaho State University/Biota Research and Consulting, Inc. ferret study team-Steven Forrest, Louise Richardson, Tom Campbell, and Denise Casey; Arthur Allen, Habitat Evaluation Procedures Group, USFWS; Wayne Brewester and Ronald Crete, Office of Endangered Spe-

Fig. 2. The relationship of habitat variables, life requisites, and cover types to the HSI for the black-footed ferret.

Model Description

Overview.—The BFF can meet its year-round habitat requirements within prairie dog colonies providing: (1) prairie dog colonies are large enough, (2) burrows are numerous enough, and (3) adequate numbers of prairie dogs and alternate prey are available. This model therefore assumes that reproducing populations of BFFs use only prairie dog colonies, and habitat evaluation based on this model considers only the life requisites provided by such colonies. BFFs do not rely solely on prairie dogs for food, but breeding populations may depend on prairie dog colonies with their host of associated vertebrates, many of which are known food items. It assumes that these colonies will provide a sufficient prey base (including alternative prey) and sufficient burrow openings for predator evasion and as sites of litter rearing, thus providing maximum potential for BFF habitat. Ecological differences in habitat

may be found if future populations of BFFs are discovered, or if BFFs are found on areas other than prairie dog colonies.

The following section documents the logic and assumptions used to translate habitat information for the BFF to the variables and equations used in the HSI model. Specifically, this section covers: (1) identification of variables used in the model, (2) definition and justification of the suitability levels of each variable, and (3) description of the assumed relationship between variables. The BFF habitat variables have been grouped into two sets: (1) an aggregated set of four variables that assess cover/reproduction as life requisites and (2) a single life requisite variable for food. Figure 2 illustrates the relationship of habitat variables, life requisites, and cover type for the BFF. The five habitat variables identified under the two life requisite categories are: $V1$ is the frequency distribution of colony sizes, $V2$ is the total area of colonies, $V3$ is burrow opening density: average number of burrow openings per ha of colony, $V4$ is intercolony distance: mean distance between colonies (these four variables are grouped under the cover/reproduction life requisite), and $V5$ is prairie dog density: mean number of prairie dogs per ha (this variable is the food life requisite). The aggregated variables are viewed as compensatory (i.e., an increase in one variable will increase the HSI, but not the suitability of other variables) and thus are combined to produce a single HSI. The limiting factor method is suggested for evaluating resulting values of the two variable sets.

Cover/reproductive component.—BFFs rely on prairie dog burrows for cover and litter rearing. Four variables are defined.

Variable 1 examines the relationship be-
tween the distribution of prairie dog colony
sizes in a region and its Suitability Index.
Prairie dog colonies present at the turn of the
century represented extremely large areas of
contiguous prairie dog distribution (e.g., in
Montana see Flath and Clark 1986). Such ar-
eas represented a 100% prairie dog occupancy
and were assumed to be optimal habitat for
BFFs. By comparison more recently, Mel-
lette County, South Dakota, showed 1.7% of
its area occupied by prairie dogs, with a mean
colony size of about 9 ha (Hillman et al. 1979).
The Big Horn Basin of Wyoming containing
the Meeteetse BFFs has about 1.7% of its area
occupied by prairie dogs in many small, low-
density colonies, although a few exceed 1,000
ha (Clark et al. *Description and history*,
1986). Clark et al. (1982) described several
sample areas in New Mexico that showed
about 1% in prairie dogs, with colony sizes
averaging 33 ha (range 10–61 ha); in Utah
about 1.9%, with colony sizes averaging 33 ha
(range 2-73 ha); in Wyoming on Thunder
Basin National Grassland about 1.3% in
prairie dogs showing a wide range in colony
sizes; in southern Wyoming about 3.2% in
prairie dogs, with colony sizes ranging up to
2,500 ha; and in another area in Utah, colonies
averaged 125 ha (range 0.2–958 ha). The total
sizes of these areas varied, and this fact clearly
influenced the distribution of prairie dog
colony size located. If a line is drawn around
the prairie dog complex at Meeteetse (least
polygon enclosing all $50+$ ha colonies) and the
area occupied by prairie dogs inside this
polygon is calculated (about 130 sq km), then
about 22% of the area is occupied by prairie
dogs. The 50 ha figure does not mean that
smaller colonies are not important to BFFs;
indeed the smaller colonies are used at Mee-
teetse (Forrest et al. 1985). Colony size distri-
bution within this area is listed in the Ap-
pendix (Table 3).

V1 is a multidimensional probability estimate
and is not graphable as are the remaining vari-
ables. The Appendix describes computation of
V1.

Variable 2 is the total area of prairie dog
colonies. Assuming a BFF MVP consists of 100
breeding adults (even though Groves and Clark
[1986], using genetic methods, estimated 200),
then 100 colonies of 50 ha each (about 5,000 ha)
is required to support them. It is assumed that
greater colony area means greater sites for
cover and reproduction for BFFs.

Variable 3 is burrow opening density: the
average number of burrow openings per ha of
colony. Colonies at Meeteetse are character-
ized by burrow opening densities as low as 10
openings/ha and up to $100+$ openings/ha.
This compares with other areas ranging
21–135/ha for black-tails, 32–57/ha for Gun-
nisons, and 2–64/ha for other white-tails
(Clark et al. 1982) . It is assumed that the
greater the burrow opening density, the
greater the cover and sites for successful rear-
ing of young.

Variable 4 is the mean of intercolony
(nearest neighbor) distances. This variable is
essential for cover/reproductive require-
ments but is also essential for expansion of
BFF populations and dispersal. In pristine
times, BFFs in large colonies may have dis-
persed from their natal areas to new areas
without ever leaving the single large prairie
dog colony. Dispersal between colonies,
where escape cover is minimal or absent, is
thought to expose BFFs to high rates of mor-
tality. Intercolony distance at Meeteetse is
about 0.92 km (range 0.13 to 3.70) . In South
Dakota intercolony distance averaged 2.4 km.
Intercolony distance for a sample of 11 Gun-
nison's colonies in New Mexico, Colorado,
and Utah was 2.4 km and for 33 white-tailed
colonies in Utah and Colorado was 4.9 km. In
winter at Meeteetse BFFs in intracolony
movements often travel $2+$ km per night
hunting. Movements up to 8 km have been
noted during the breeding season. It is as-
sumed that the smaller the intercolony dis-
tance, the higher the quality of BFF habitat.

Food component.—Food is described by a
single variable.

Variable 5 is prairie dog density (number/
ha). High densities of prairie dogs provide
increased opportunity for BFFs to success-
fully meet their energy and nutrient require-
ments as well as providing alternate prey asso-
ciated in prairie dog colonies colonies.
Additionally, a high density of prairie dogs
means an increased density of burrows, which
is related to the previous variables as well.

TABLE 1. Equations for determining year-round life requisites for the black-footed ferret (2.0 is included as a scaling factor).

Life requisites	Cover type	Equation
Cover/Reproduction	All cover types where prairie dog colonies occur	$(2 \times V1 \times V2 \times V3 \times V4)^{1/4}$
Food	Same as above	V5

Variable Relationships

Suitability of BFF habitat depends entirely on attributes of prairie dog colonies. V1 converts the distribution of colony sizes (relative to the total colony area) into a single SI measure. V2 accounts for the total area of colonies relative to BFF requirements and is especially discriminative in the range of MVP area size. V3 gauges the value of colonies in terms of cover (burrow opening density) and, although it generally covaries with food (V5: prairie dog density), any particular case may be critically uncorrelated. V4 (intercolony distance) appraises the effect of colony dispersion in reference to BFF mobility and behavior. In summary, V1 reflects colony size distribution, V2 the total colony area the size distribution represents, V3 the cover value of the colonies, V4 the spatial dispersion of those colonies, and V5 the food value of the colonies.

Suitability Index (SI) graphs and equations for habitat variables.—This section contains suitability index graphs and equations that illustrate the habitat relationships described in the previous section (Fig. 2).

Equations.—Life requisite values for the BFF can be obtained by combining the SI values through the use of equations (USFWS 1981). A description and explanation of the assumed relationship between variables was included under the Model Description, and the specific equations in this model were chosen to mimic those perceived biological relationships as closely as possible. The suggested equation for obtaining year-round life requisite values for the BFF are given in Table 1. The four cover/reproduction variables are multiplied by two (a scaling factor for V1) and aggregated by using the geometric mean, GM. We necessarily use the GM because the quantities involved are measured on a ratio scale and the variables are not arithmetic sequences but geometric.

VARIABLE

V1 Distribution of colony sizes,

$$P(AB|N_i, i) = \frac{\sum_{i=2}^{k} N_i \binom{i}{2}}{\binom{\sum_{i=1}^{k} N_i \times i}{2}}$$

With n_i as the number of colonies of size i, the resulting probability increases nonlinearly with increase in colony sizes (numerator) relative to the size of the complex (denominator)(see Appendix for example calculations of this equation)

VARIABLE:

V2 Total area of colonies,
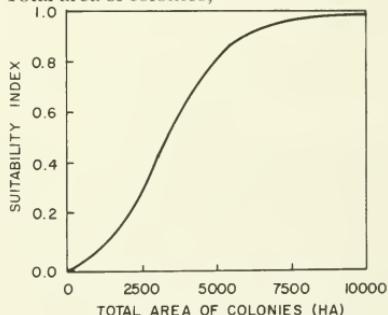
V3 Burrow opening density (mean number of burrow openings/ha of colony),
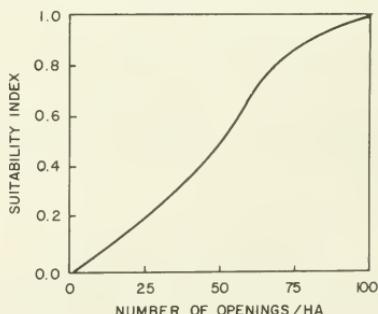
V4 Intercolony distance (mean distance be-
tween colonies),
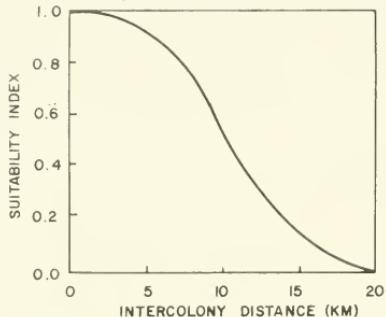
V5 Prairie dog density (mean number of
prairie dogs/ha of colony),
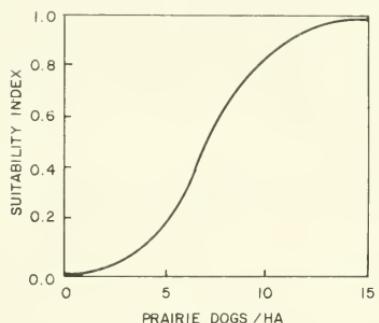
HSI determination. —The HSI for the BFF
will equal the lowest of the SI values obtained
for either the Cover/Reproduction or Food
life requisite. This recognizes limiting factors.
The fact that V2 only scales to 10,000 ha of
total colony area reflects the importance of an
MVP area and does not mean that even
greater-sized prairie dog complexes are not
more desirable. The larger the complex the
better. The largest complex sizes available
should be selected for BFF translocations,
and these should exceed the size of Meeteetse
(Appendix). An HSI approaching 1.0 is ideal
and not necessarily attainable; that is, a math-
ematical ideal or extreme to compare
against—in actuality, perfect habitat does not
exist.

Application of the Model

Definitions of variables and suggested field
measurement techniques are presented in

Table 2. Vegetative cover types for each vari-
able are those that contain prairie dog
colonies. The Appendix contains HSI calcula-
tions for Meeteetse and two other areas.
These are presented as examples of model
application, for ease of application of HSI to
other areas, and for comparative purposes.

Interrelationships

Three considerations from application of the
HSI format to the Meeteetse BFF environ-
ment as described in the Appendix must be
addressed. First, the Meeteetse HSI of 0.590
for the cover/reproductive variables is
midrange in a HSI range of 0–1. Prairie dog
complexes should be located that exceed the
Meeteetse HSI and that can support large
BFF populations well above the MVP. It is
the low V2 (complex size or total colony area)
that deflates the overall HSI. Second, if high
HSI areas cannot be located that can support a
MVP, then a series of smaller areas showing a
lower HSI than Meeteetse will have to be
utilized in a complex, complementary, and
closely managed situation. Third, application
of the HSI format to the prairie dog area in
Mellette, South Dakota, may show that its
HSI is well below estimated MVP require-
ments. If so, this means that management for
a minimum area and colony size pattern as
suggested by Hillman et al. (1979) has been
below the area needed to sustain a MVP of
BFFs and that new recommendations are
needed.

Sources of Other Models

No habitat models for the BFF were located
in the literature except for descriptions of
BFF habitat by Hillman et al. (1979), Strom-
berg et al. (1983), and Forrest et al. (1985).

Concluding Remarks

If the prairie dog colony size distributions
shown in Table 3 of the Appendix are typical of
prairie dog complexes, then in terms of prairie
dog complex area, the sum influence of most
colonies will be less than the few very large
ones. Distributions with this property of ag-
gregation or clumping are called contagious
and can often be modeled by generalized dis-
crete distributions (reviews in Coleman 1964,

TABLE 2. Definitions of variables and suggested field measurement techniques.

	Variable definition	Suggested technique
V1	Frequency distribution of colony sizes (all inhabited by prairie dogs)	Accurately map colony configurations, determine colony areas from maps; ground surveys are best, but some preliminary aerial surveys may be needed first
V2	Total area of colonies (all inhabited by prairie dogs)	Total area of all colonies in the study area based on accurate mapping determined for VI
V3	Burrow opening density (number/ha of colony)	Walk colonies and count holes, or sample selected areas
V4	Intercolony distance (mean distance between colonies)	Measured from the edge of a mapped colony along the shortest distance to the next nearest colony
V5	Prairie dog density (mean number of prairie dogs/ha of colony)	Use minimal visual counts of prairie dogs active .5–2 hrs after sunrise on three consecutive mornings in mid-June; live capture-mark/recapture population estimate in mid-June

Douglas 1979). If we view the colonies in a prairie dog complex distributed as a Poisson variate and assume the number of ha per colony has a highly nonrandom logarithmic distribution, then we may obtain the Poisson-logarithmic compound distribution (a type of negative binomial). However, the colony size distributions could not be fit to this distribution even when larger colonies were ignored. This illustrates the extreme "contagion" of prairie dog aggregation and, consequently, the disproportionate effect of such large clusters on the outcome of any realistic model concerning BFF MVPs.

In conclusion, from a statistical standpoint, the most effective and, therefore, most intensive and accurate data collection could be concentrated in the large colonies (in fact, as a nonlinear function of size) with little loss of accuracy. In other words, the model is very robust to small colony exclusion. Indeed, for all variables except V4, which equally weights colony location and therefore dispersion effect, small colonies could be ignored for data collection in MVP-sized complexes when considering cost and time budgeting.

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APPENDIX

Calculations of HSI for Meeteetse and two Other Areas

Variable values are most often arrived at by sampling techniques which produce confidence limits. In addition, stratified sampling or consideration of subsets of an area may produce a large range of possible variable values for calculation. For ease of computations and sensitivity analysis, the equations for Vl-V5 are given below and are easily computed on handheld calculators.

Structure of V1

Colony size has been stressed in terms of successful reproduction and energetics. V1 appraises this important aspect of colonies by producing higher values for size distributions containing larger colonies and disproportionately lower values for a distribution (given the same area) containing smaller colonies. The following analogy may improve our understanding of this. Assume we have two BFFs, A and B, and wished to distribute them on their own one-hectare plot in a number of Total Areas, each of which contains a different number of colonies totaling a constant area. We drop the two BFFs randomly over these areas and note where they fall. In areas containing a few large colonies, BFFs A and B are noted to land more often on the same colony; in areas of many small colonies, A and B rarely share the same colony. Formally, if we divided a sample space (Total Area) into n subspaces (colonies) where 1 to k are colonies of size i and N_i is the number of colonies of size i, then the probability of any two objects (BFFs A and B) co-occurring in the same subspace (colony) is

$$P(AB|N_i, i) = \frac{\sum_{i=2}^{k} N_i \binom{i}{2}}{\binom{\sum_{i=1}^{k} N_i \times i}{2}}$$

Since $\binom{x}{2} = \frac{x!}{2!(X-2)!} = \frac{x^2 - x}{2}$, then

$$P(AB|N_i, i) = \frac{\sum_{i=2}^{k} N_i (i^2 - i)}{\left(\sum_{i=1}^{k} N_i \times i\right)^2 - \sum_{i=1}^{k} N_i \times i}$$

In reduced form, solving for $P(AB|N_i, i)$ is simply combining two summations. Summate $N_i (i^2 - i)$ and store in memory M_1. At the same time summate $N_i \times i$ and store in memory M_2, then calculate

$$\frac{M_1}{M_2{}^2 - M_2}.$$

TABLE 3. Colony sizes for Meeteetse (Area I), another prairie dog complex (Area II), and a hypothetical complex (Area III). The frequency distribution is in order of colony size and grouped in three size class frequencies.

Colony numbers	Colony sizes in hectares		
	Area I	Area II	Area III
1	.5		
2	.5		
3	.5		
4	1.0		
5	1.5		
6	2.0		
7	2.5	3	
8	2.5	4	
9	3.0	5	
10	3.5	6	0–25
11	5.0	7	
12	6.0	8	
13	8.5	10	
14	9.0	11	
15	9.5	12	
16	11.0	14	
17	12.5	15	
18	20.5	19	
19	21.0	20	
20	24.0	21	
21	24.5	22	
22	26.5		
23	30.5		
24	31.5	31	25–50
25	31.5	34	
26	49.5	49	
27	50.5	67	
28	51.5	81	
29	69.5	87	
30	97.5	143	
31	102.0	151	
32	153.0	231	>50
33	183.0	257	
34	196.5	617	200
35	211.0	658	2100
36	230.0	671	2200
37	1307.0	2242	2300
Total area	2990	5496	6800
Total colonies	37	29	4

All colonies <1 ha are entered as 1 ha. Since colony sizes are often unique numbers or are entered that way as data, then N_i is completely eliminated from the calculations (see example). However, if each colony area is not estimated for some reason, then they can be grouped into intervals such as 0–5 ha, 5–10 ha, etc., in which case the midpoint can be used (i.e., 2.5, 7.5).

Structure of V2–V5

Variables 2, 3, 4, and 5 are intrinsically non-linear and are each derived from the differential equation $dy/dt = ay^2 + by + c$ and simplified to the logistic form of

$$Y = (1 + ke^{-rt})^{-1}$$

The logistic form is particularly suitable in describing these variables because it depicts two asymptotic limits (at 0 and 1 adjustable toward infinity) and contains an inflection point around which the most rapid rate changes occur. For example, intercolony distance (V4) reflects the ability of BFFs to intercept life requisites upon leaving one colony for another. If a straight-line 10 km is as much as BFFs might move in a night, then that value is the inflection point around which critical and therefore extreme shifts in the suitability index (SI) occur. Of course, BFFs easily move from 0 to 5 km and SI values change little within that range. Likewise, once a BFF is well past the "point-of-no-return," say 15–20 km, SI value shifts are also small. Another view is that the chance of intercepting another colony along a radius extending from its home colony is a quadratic function of distance moved modified by the actual mobility and energetic characteristics of the BFF.

V2: $f(x) = (1 + 20 e^{-.0009x})^{-1}$	x ha
V3: $f(x) = (1 + 15 e^{-.06x})^{-1}$	x burrows/ha
V4: $f(x) = 1 - (1 + 70 e^{-.4x})^{-1}$	x km
V5: $f(x) = (1 + 200 e^{-.8x})^{-1}$	x prairie dogs/ha

Examples of HSI Calculations

Table 3 contains colony sizes for the Meeteetse complex (Area I), an actual prairie dog complex elsewhere (Area II), and a hypothetical area (Area III). Maps of these three areas follow (Fig. 3). Before computing VI with this data, it is important to understand that although Area I and Area II have different distributions of absolute colony size, the distributions are quite similar in colony size relative to their total colony area. It is V2 that will account for the almost double total area of Area II.

V1: First, calculate

$$\sum_{i=2}^{k} N_i (i^2 - i).$$
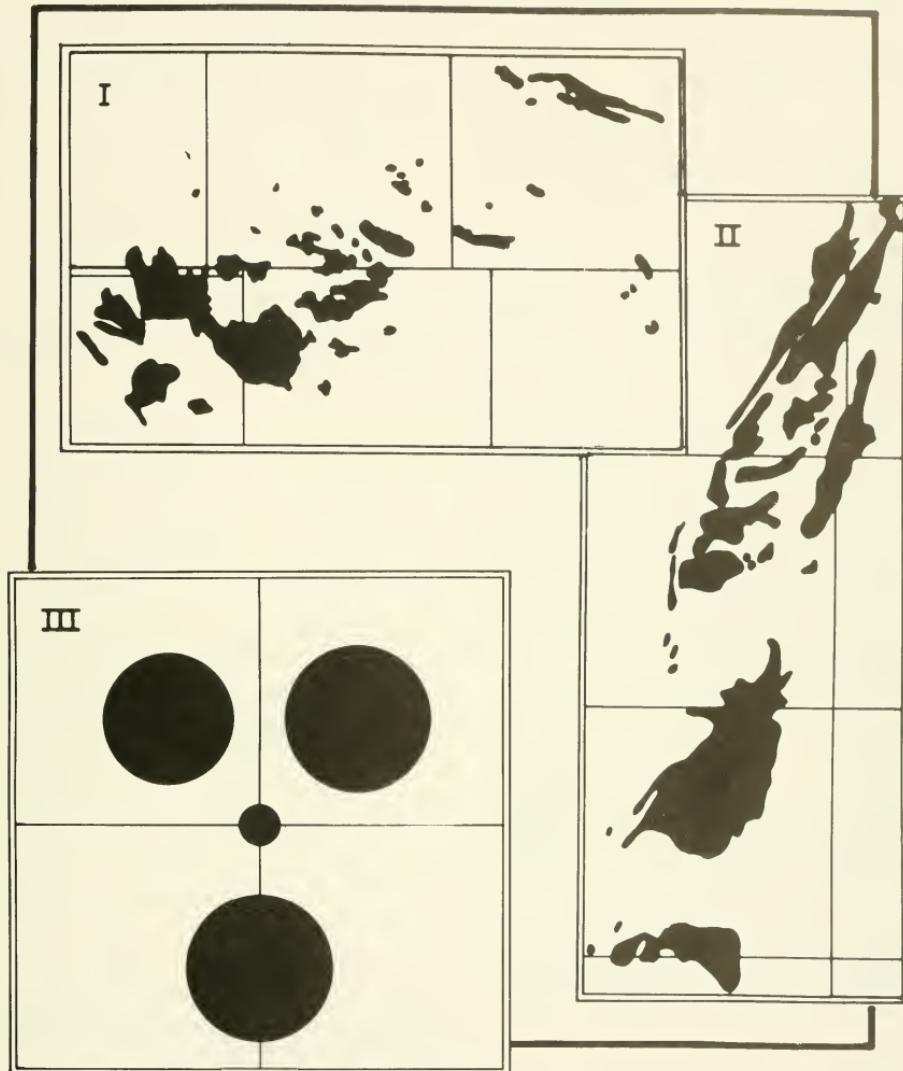
Fig. 3. Maps of prairie dogs complexes used in examples of calculations of HSI. Area I = Meeteetse, Wyoming, Area II = another actual complex, Area III = hypothetical complex.

Since each colony has a different area, N drops out and we add the following series for Table 3 showing colony sizes for each area:

Area I: $(1.5^2-1.5) + (2^2 - 2) + ... + (230^2-230) + (1307^2-1307) = 1,936,862$

Area II: $(3^2-3) + (4^2-4) +... + (671^2-671) + (2242^2-2242) = 6,473,430$

Area III: $(200^2-200) + (2100^2-2100) + (2200^2-2200) + (2300^2-2300) = 14,573,200$

Note that we do not include areas of size 1; $1^2 - 1 = 0$.

Second, calculate which is really only the total colony area manipulated as in the first calculation:

$$\left(\sum_{i=1}^{K} N_i \times i \right)^2 - \sum_{i=1}^{K} N_i \times i,$$

Area I: $2990^2 - 2990 = 8,937,110$
Area II: $5496^2 - 5496 = 30,200,520$
Area III: $6800^2 - 6800 = 46,233,200$

We arrive at V1 by dividing the first by the second calculations for each area: $V1 = P(AB)$ = .217 for Area I, .214 for Area II, and .315 for Area III.

Notice the influence of Area I and II's largest colony on the outcome of the first calculation. Area I: $1307^2 - 1307 = 1,706,942$ and for Area II: $2242^2 - 2242 = 5,024,322$. If we were to split Area I's 1307 ha colony into two separate colonies, it would decrease the value of V1 to .131. How far apart these colonies would be is accounted for by a simultaneous increase or decrease of V4. For instance, note how the small 200 ha colony in Area III is a stepping stone between the three larger colonies. Its critical position is reflected by a lower mean intercolony distance and therefore a higher value for V4.

Graphs of the variable equations and the above values follow.

Completing the other values we obtain:

Variable	Area I	Area II	Area III
V1	.217	.214	.315
V2 (ha)	.424 (2990)	.876 (5496)	.958 (6800)
V3 (burrows/ha)	.671 (57)	.385 (37.3)	.992 (125)
V4 (km)	.980 (.92)	.980 (1)	.969 (2)
HSI =	.590	.613	.873
V5 (dogs/ha)	.214 (5)	.155 (4.5)	.987 (12)

HSI for:
Area I $= (2 \times .217 \times .424 \times .671 \times .980)^{1/4} = .590$
Area II $= (2 \times .214 \times .876 \times .385 \times .980)^{1/4} = .613$
Area III $= (2 \times .315 \times .958 \times .992 \times .969)^{1/4} = .873$

VARIABLE

V1 Distribution of colony sizes

$$P(AB|N_i, i) = \frac{\sum\limits_{i=2}^{K} N_i \binom{i}{2}}{\left(\dfrac{\sum\limits_{i=1}^{K} N_i \times i}{2}\right)}$$

Using the above equation for V1, area I = .217, Area II = .214, and Area III = .315.

V2 Total area of colonies
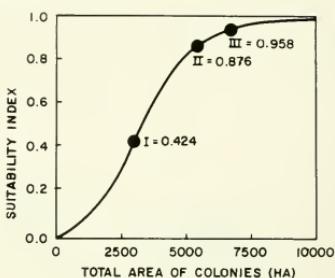
V3 Burrow opening density (mean number of burrow openings/ ha of colony)
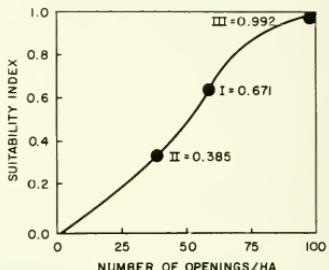
V4 Intercolony distance (mean distance between colonies)
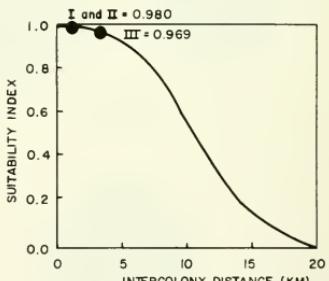
V5 Prairie dog density (mean number of prairie dogs/ha of colony)
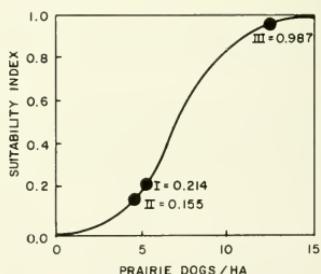
DESCRIPTIVE ETHOLOGY AND ACTIVITY PATTERNS OF
BLACK-FOOTED FERRETS

Tim W. Clark[1], Louise Richardson[1], Steven C. Forrest[1], Denise E. Casey[1], and Thomas M. Campbell III[1]

Abstract. —Aspects of the aboveground ethology and activity patterns of the black-footed ferret (*Mustela nigripes*) are described for a population in northwestern Wyoming as a first step in building a descriptive ethogram and quantification of activity patterns. We observed at least 237 individual ferrets for 208 hr on 441 occasions from 2 December 1981 through 25 September 1984. Maintenance behaviors (locomotion, alert, grooming and sunning, defecation and urination, digging, and predation) and social behavior (reproduction, ontogeny, maternal, play, agonistic) are described as well as some ferret-human interactions. Ferret vocalizations are subjectively described. We located ferrets during most months, including winter, but found that they were easiest to locate in summer. Ferrets were active at -38 C, in snow, in rain, and in winds to 50 kph.

The black-footed ferret (BFF) is one of the least well known of all the endangered mammals in the United States despite 11 years (1964–1974) of intensive and extensive research in South Dakota (Erickson 1973, Hillman and Linder 1973). Data are lacking on many aspects of BFF behavior and activity patterns. It is essential that the general behavior patterns of any animal first be qualitatively described in an "ethogram" to provide the basis for more specific, quantitative behavioral studies (Scott 1956, Klopfer and Hailman 1967, Lehner 1979). This paper provides an initial description toward a BFF ethogram and gives results of nocturnal observations of surface activity for the Meeteetse, Wyoming, BFFs. Behavioral descriptions are "functional" (Candland 1974) and definitions are operational (Sustare 1975).

METHODS

Behavioral descriptions are based on 208 hr of direct observation of at least 237 individual BFFs on 441 occasions between 2 December 1981 and 25 September 1984. We observed maternal, play, and predatory behavior at 10 m or less, sometimes for over 1 hr per observation. Daytime observations were generally made with the unaided eye, but a spotting scope and binoculars were sometimes used. Nighttime observations were made with the aid of hand-held or truck roof-mounted spot-

lights following methods outlined by Clark et al. (*Handbook of methods*, 1984). The time and duration of each observation, description of behavior, and weather conditions were recorded, and photographs were taken when possible. Because BFFs are nocturnal, secretive, solitary, and active above ground briefly and irregularly and because they inhabit an environment of grass and shrubs, it is very difficult to observe and collect a complete picture of their ethology. Some BFF behavior (e.g., locomotor, predatory) was in part inferred from 243 BFF snow-tracking records collected over three winters 1981–1984 (Richardson et al. 1985 and unpublished data). Our behavioral descriptions were facilitated by earlier behavioral observations (by TWC) of steppe ferrets (*M. eversmanni*, 32 hr) and European ferrets (*M. putorius*, 123 hr), as well as by ethological studies on other species. Where appropriate, we compare our observations with the literature on BFFs and other mustelids.

RESULTS

We describe individual maintenance, intraspecific social, and interspecific behavior patterns (the three major behavioral categories often recognized; e.g., Balph and Stokes 1963), as well as BFF vocalizations. Photographs of some of these behaviors and BFF signs are in the Appendix.

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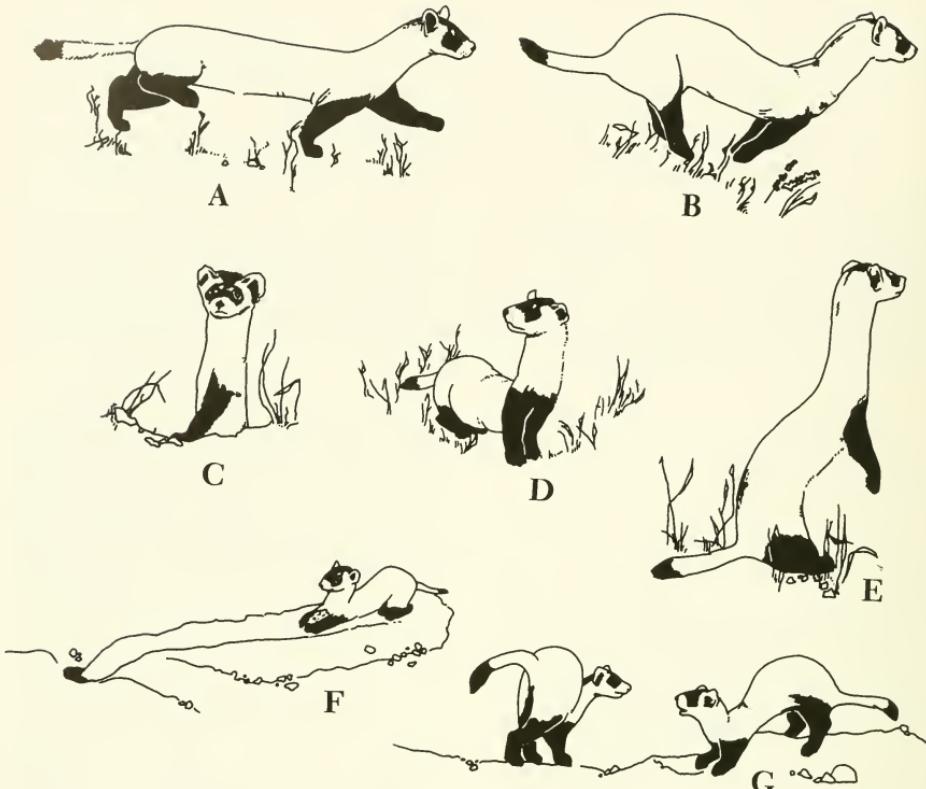
Fig. 1. Some black-footed ferret motor patterns and body postures: A, Walking. B, Bounding. C, In-burrow alert posture. D, All-fours alert posture. E, Upright alert posture. F, Digging, G, Play.

Maintenance Behavior

Maintenance behavior is performed by an animal in the normal course of its daily activities and is critical to its survival.

Locomotion.—BFFs either walked or bounded (Fig. 1). Walking is a forward progression in the typical quadruped manner—a cross-wise stepping movement. Forward movement of the left front leg was followed by the right hind leg, then the right front leg was followed by the left hind leg. The head was usually held above the torso but was occasionally lowered as if to sniff the ground. The tail was usually held off the ground, at a variable downward angle from the torso. BFFs walked about 2% of the distance traveled per winter night, typically near prairie dog burrow entrances.

Bounding is a leaping run or gallop in which both hind feet and then both front feet are alternately set before one another, with the hind feet set fairly accurately in the twin tracks of the front feet. Travel between prairie dog (*Cynomys leucurus*) holes and long distance movements were in this gait. BFFs often traveled in vegetation-free areas such as cattle and game trails, roads, snow-filled gullies, and windblown hill crests. Relatively straight line movements of 75 m were common.

Hillman (1968), Henderson et al. (1969), and Fortenbery (1972) described BFF movements between prairie dog burrow openings as "running." They did not describe walking or bounding locomotion; however, photographs of BFF tracks in snow in Fortenbery (1972) were the bounding type.

Alert behavior.—Alertness composed a high percentage of BFF behavior and was the only activity that frequently interrupted all others. Alertness was characterized by: (1) in-burrow alert posture ("periscope"), in which only a BFF's head, part of the head, or upper torso was visible; (2) down alert posture, aboveground alertness in which all four feet were on the ground; and (3) upright alert posture, in which the BFF stood on its hind feet, balancing with its tail and hind legs, with its forelegs off the ground (Fig. 1). An immobile body was the common element of the different alert postures.

The in-burrow alert posture or periscope was by far the most common alert posture. The down alert often occurred between bursts of locomotion, especially if the BFF was hunting in tall vegetation with the prairie dogs active nearby. The upright alert posture was less frequently observed under similar circumstance and was of very short duration.

Alert postures have not been described for BFFs. However, Fortenbery (1972) noted that BFFs may look out of prairie dog burrows, with only their heads showing (our in-burrow alert). The limited descriptions and photos in Henderson et al. (1969:7,11) and Fortenbery (1972) suggest that the BFFs in Wyoming and South Dakota have similar repertoires of alert postures.

Grooming and Sunning.—BFFs scratch, mouth, and bite at their fur. These activities are functionally related to dressing the pelage, cleaning the body surface, and removing parasites (Eisenberg 1968). Scratching (n=8) consisted of perpendicular movements of one hind leg directed at various points on the body. Mouthing movements (n=4) are complex and variable and consisted of "biting" fur on the tail, legs, and ventral and lateral areas of the torso. Grooming of fur was evidenced by BFF hairs found in BFF scats. Washing or licking were not seen. Ticks were relatively common behind the ears, on the upper neck, and under the chin of adult BFFs. BFFs bit at flies that flew near their faces. We also observed BFFs yawn while sunning, where the head is thrown back, mouth opened full gap, and eyes closed.

Henderson et al. (1969) noted that an adult female BFF scratched a scab on her head with her hind paw and that young and adult BFFs seemed bothered by external parasites (ticks, fleas, and flies) and frequently scratched themselves. However, motor patterns were not described. Henderson (personal communication 1983) observed BFFs in South Dakota yawn.

Sunning consisted of lying sternally stationary on prairie dog mounds in sunlight. We observed this three times in midsummer between 0800 and 1100 hrs Henderson et al. (1969) noted that adult BFFs often basked in the warm, midmorning sun for several hours on prairie dog mounds during the young care period (July-August), fall, and spring. Progulske (in Henderson et al. 1969:7) reported sunning behavior in a captive adult male BFF. Henderson (personal communication 1983) observed BFFs basking in the sun in the snow.

Defecation and urination.—About 75 scats of possible BFF origin and an additional 15 of known BFF origin were found from December 1981 to January 1984 and are shown in Clark et al. (*Handbook of methods*, 1984). Of scats of probable BFF origin, two were found on top of each of two badger (*Taxidea taxus*) scats, several on BFF diggings, five beside a frozen BFF corpse in February 1982, and nearly all others near prairie dog burrow openings. Urinations (n=114) along snow-track routes were generally located near burrow entrances but did occur in midroute (Richardson et al. unpublished data).

Henderson et al. (1969) noted that scats and urinations were deposited separately, usually near a burrow mound, but the salient feature of BFF scats is that they are seldom found (Hillman 1968, Henderson et al. 1969, Fortenbery 1972). Hillman (1968) assumed and Henderson et al. (1969) suspected that BFFs defecate underground. Droppings of a captive adult male BFF were deposited in one corner of the pen during summer and in the burrow box during winter (Progulske 1969). Sheets and Linder (1969) recovered BFF scats from prairie dog burrows they excavated by machine.

Digging behavior.—BFFs excavate subsoil from prairie dog burrows and deposit it in a distinctive manner (Hillman 1968, Henderson et al. 1969, Hillman and Linder 1973, Hillman and Clark 1980, Clark et al. *Seasonality of black-footed ferret diggings*, 1984) (Appendix). We watched BFFs dig on nine
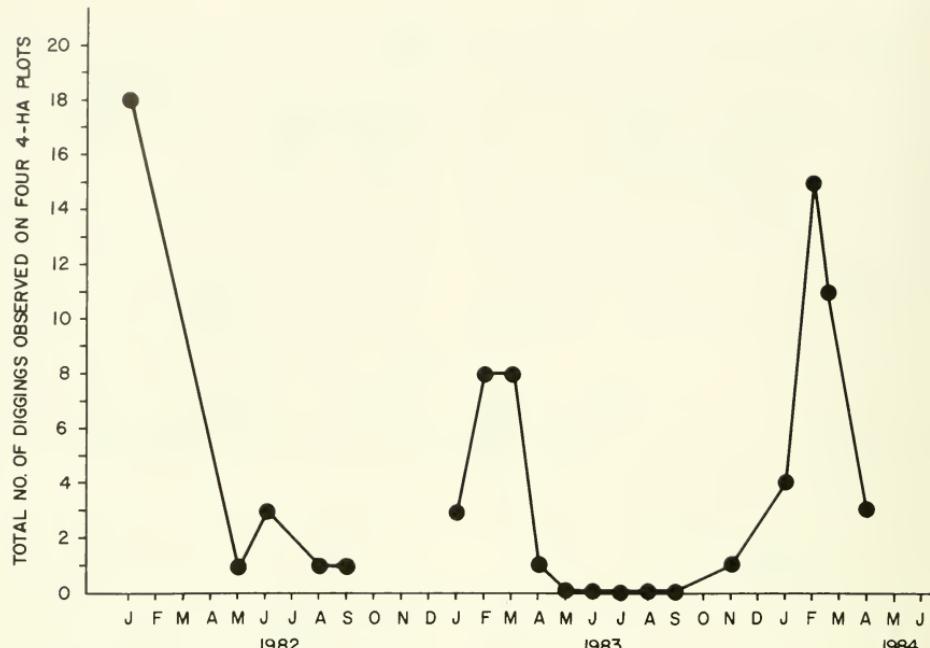
Fig. 2. Total number of ferret diggings observed on four 4-ha (16 ha) plots within the Meeteetse black-footed ferret habitat.

occasions, including the formation of two "diggings" or "trenches," as these structures were usually labeled by earlier observers. We prefer the word "diggings," since the subsoil is piled on the ground outside a prairie dog burrow and not dug into the soil surface as implied by the term "trench." When digging in a prairie dog burrow, BFFs back out of the tunnel with loosened subsoil held against their chests by their front feet. They drag the material further from the entrance with each trip (Fig. 1). The subsoil is sometimes pushed under the BFF's body, which may then arch forward, with the hind feet kicking soil further backward (pictured in Henderson et al. 1969: 15). BFFs also dig furrows in snow several centimeters deep, but we have not observed how these are made.

We observed results of BFF digging mostly during winter, when white-tailed prairie dogs were hibernating, but evidence of BFF digging was noted during all other seasons (Clark et al. *Seasonality of black-footed ferret diggings*, 1984; Clark et al. *Handbook of methods*, 1984) (Appendix). The frequency of occurrence and density of BFF diggings were

seasonally marked on four, four-ha plots (Fig. 2). BFF diggings may be related to food acquisition. Seasonal peaks in diggings that could be identified as BFF occurred January-March and dropped to near zero by May each year. Both peaked in January, based on samples taken from January through December 1982, as described by Clark et al. *Seasonality of black-footed ferret diggings*, 1984; Clark et al. *Handbook of methods*, 1984) at about 4% and 2.5/ha, respectively, then dropped to near zero in April and remained very low until October, when they began to increase. South Dakota researchers agree that winter is the best time to look for BFF diggings: Hillman (1968) reported seeing BFF diggings in snow. Fortenbery (1972) noted that BFF diggings made during winter may persist for a long time. Henderson et al. (1969) observed more diggings in winter and in areas with small prairie dog populations. The excavated material may have been previously excavated by prairie dogs and subsequently brought to the surface by BFFs. The function of digging snow trenches is unknown. Hillman (1968) and Henderson et al. (1969) concluded that no

other mustelid that visits prairie dog colonies digs or leaves subsoil deposited in a manner like BFFs, but other mustelids and prairie dogs do excavate subsoil. An adult female BFF on 8 August 1983 moved eight stones (seven about 2.5 cm in diameter and one about 12 cm long, 5 cm wide, and 2 cm thick) from the burrow mound into her burrow over 22 mins. Each stone was individually moved, in the cases of the seven small stones, with the mouth, and the single large stone was dragged with the forelegs. The function of this activity is unknown.

Predatory behavior.—BFFs presumably obtain prey mostly at night below ground inside prairie dog burrows. Our snow tracking indicated that, in addition to taking prairie dogs, BFFs also take small rodents (*Peromyscus maniculatus*), and lagomorphs. During daylight in summer we saw BFFs kill prairie dogs and drag them to other holes on five occasions. During summer, one BFF leaped 0.7 m onto an adult prairie dog emerging from a hole and bit the back of the prairie dog's head. The BFF and prairie dog fell down inside the hole during the struggle. Two minutes later, the BFF emerged holding a prairie dog by the throat. The kill was dragged 10 m to a hole containing at least part of the female BFF's litter. Nine prairie dogs were on the surface within 40 m just prior to the kill. Another BFF ran 10 m to, and descended down, a hole that a prairie dog had just descended. The upper body of the prairie dog emerged from the hole but apparently was dragged back down by the BFF biting its posterior. Two minutes later the BFF emerged dragging a dead prairie dog by its throat. On two occasions, a BFF ran up to a prairie dog burrow opening, stopped with its body head first halfway down the hole, and waited motionless about 4 mins. At this time, the BFF dove into the tunnel, and prolonged high-pitched prairie dog "screams" and BFF "growls" emanated from the tunnel. On both occasions, the BFF emerged with a dead prairie dog within 5 mins. In all the above cases of predation, the prairie dog prey had a bloody throat and no other observable wounds.

On one occasion, a BFF bounded through the tall grass and shrubs and flushed out a ground squirrel (*Spermophilus armatus*). Within three additional bounds the BFF

leaped on the back of the fleeing squirrel and seized it with a bite to the base of the skull. The BFF then descended a nearby ground squirrel burrow carrying the dead squirrel. Another BFF dragged two juvenile prairie dogs, one at a time, near us and dropped one. The killing bite appeared to be between the shoulder blades. Another time, a BFF ran toward a prairie dog 5 m away above ground but did not enter the hole the prairie dog retreated down.

BFFs are active in winter, exploring various burrows along their movements. Once a BFF enters a burrow, presumably it locates and captures prey by sound and smell. It sometimes takes prey above ground away from burrows. BFFs may remain below ground for several days in the same hole (Richardson et al., unpublished data). Prey were apparently often consumed below ground in burrows where kills were made. BFFs dragged prairie dog carcasses to another hole. One such kill found along a BFF drag exhibited punctures and hemorrhaging in the neck area behind the head (Appendix). In winter BFFs do not use any one burrow as a long-term nest burrow and may use some burrows as "cache" burrows (Richardson et al., unpublished data).

Our observations of BFF "hunting" behavior and those described by Hillman (1968), Henderson et al. (1969), Hillman and Linder (1973), and Fortenbery (1972) indicate that the BFF is a "searcher" predator (Alcock 1975). Our observations and those by Hillman (1968), Henderson et al. (1969), and Progulske (1969) in South Dakota are similar and suggest that killing behavior is stereotyped. BFFs kill both young and adult prairie dogs (Hillman 1968). Progulske (1969) observed a prairie dog bite an adult male BFF on the face. The facial cuts on BFFs we saw could have been inflicted similarly.

Social Behavior

Social behavior refers to the interaction of two or more conspecifics. Interaction means that the animals are mutually influencing one another through some form of communication system (Eisenberg 1968).

Reproductive behavior.—We did not observe this, but snow tracking suggested that breeding activity began in mid-February and continued through March (as calculated from

the timing of litter emergence, estimated pre-emergence occupancy (45 days), and known gestation of 42–45 days (Hillman and Carpenter 1983). The initiation of reproductive activity in spring is further supported by the fact that an adult male BFF road-killed in early March near our main study area showed testicular mitotic activity but no spermatozoa, indicating that spermatogensis was just beginning (Thorne 1982, personal communication). Also in February and March, we noted BFF movements tended to increase as did activity area sizes and marking (Richardson et al., unpublished data) (Appendix). In South Dakota the exact timing of mating was unknown (Henderson et al. 1969), but captive BFFs bred in March and early April (Hillman and Carpenter 1983). Breeding behavior in captivity is described by Hillman and Carpenter (in Hillman and Clark 1980).

Ontogeny of young and maternal behavior.—The duration of time that young BFFs remain in the natal burrow before emerging above ground is unknown but is estimated at about 45 days. On 28 June 1982 a female moved a three-kit litter about 20 m from one hole to another. She carried one kit at a time in her mouth in three trips totaling 15 mins. The young were quite small (est. 200 g). In mid-July young in 11 litters appeared half- to three-fourths grown (est. 400–500 g). Nothing is known of BFF development between birth and first appearance above ground.

Mother BFFs may interact in a variety of ways with their young. In July, shortly after young began appearing above ground, mother BFFs commonly pulled young BFFs out of a burrow with her teeth and dragged them by their napes to other holes. On 11 July 1984 we watched a female with four half-grown young at a burrow. Generally the young crawled on their bellies (eyes barely reflecting our spotlight) in an area around the female while she remained standing alert watching our spotlight. At times they would all go down a nearby prairie dog hole, but reappeared three times. One time, she stood on all four feet exceptionally still while the young crawled all over her especially at her belly (nursing ?) and this lasted about three minutes. Until late July, while probably still nursing, females "coaxed" up to four young out of a burrow and led them single file in

"train behavior" (also noted by Henderson et al. 1969) across the prairie to a new site. On four occasions in July females brought dead prairie dogs to their young. On several occasions when a litter was above ground, the mother vocalized, after which all young rapidly descended into the burrow. When young are older, from late July to early August, litter mates are often seen separated—either in separate holes or one traveling with the female. On our approach she typically brought the group together by retrieving a lone juvenile or bringing the juveniles with her to the other juveniles and then keeping them all down, while she watched us.

Play.—Young BFFs in play were very quick with a variety of flexible, elastic body movements (Fig. 1). They played at night and in daylight. Play was the most often observed social behavior and was common in late July and early August. We categorized the types of play (1) object play, (2) autoplay, and (3) social play (even though the first two types are nonsocial, they are included here for completeness of play descriptions). In object play young BFFs exhibited close orientation and visual, oral, or olfactory inspection or manipulation of physical objects. One young BFF repeatedly "attacked" marker flags by jumping at them, front legs extended and mouth open.

In autoplay young BFFs moved forward and backward, with legs sometimes down together, back arched, chasing their own tails while turning their bodies around and around, rolling over on the ground, and changing position by "snapping" their bodies into the air at split-second intervals.

In social play two or more young BFFs engaged in approach-withdrawal (noncontact) or rough-and-tumble (contact) play, with the recipient of the play initiation either avoided or joined (Fig. 1). In approach-withdrawal play they constantly alternated distance between themselves as they chased and bounded forward and backward. The role of the pursuer and pursued were frequently interchanged within a single session. In these encounters mouths were sometimes open, the head was held from above to below the height of the shoulders, the tail was often extended with hairs erect, and the back was arched high (Fig. 1). No vocalizations were heard, possibly be-

cause we were too distant to hear them. This form of play occasionally followed or preceded rough-and-tumble play, in which young BFFs bit and tumbled with their interlocked bodies rolling about. Play activity occurred on and off burrow mounds and lasted up to 20 mins.

Young BFFs also exhibited a "stiff-legged dance" form of play in which they alternated approach-withdrawal among themselves and once toward a human. The limbs were alter nately stamped against the ground, first one or both front feet and then one or both hind feet.

Hillman (1968) noted that young BFFs played above ground, running in and out of burrows in pursuit of one another. They bit and pulled at each other, humped their backs, and ran on their toes, often turning in circles, attempting to bite their tails. Henderson et al. (1969) noted one young BFF executed a midair somersault similar to what we observed.

Scent-marking.—Scent-marks have been observed in the snow (Richardson et al., un published data), but marking behavior is rarely observed (Appendix). One adult male was observed marking near a burrow opening in July 1984. On a grass substrate, he dropped his pelvic region on the ground with his tail extended straight behind him, the tip about 12 cm off the ground. He moved forward about 20 cm, mainly using his forelegs while dragging and wiggling his pelvic region against the substrate. He then scraped back ward with his hind feet about four times over this area. This behavior was repeated twice more in two different grassy areas. After that, he moved to a small bush over which he ex tended his whole body, such that the neck, abdomen, and pelvis were rubbing into and wiggling through the bush. After a vigorous rubbing, he moved his forelegs and abdomen off the bush, leaving his pelvic region on the bush and rubbing into it another 3 sec. He circled around and repeated this marking be havior on the same bush two more times. The BFF may also have urinated on the bush dur ing the rubbing procedure. Each marked area exuded a strong musk odor. This behavior may have been in response to the observer standing 5 m away. After the marking behav ior, the BFF moved away slowly to explore new burrows.

Agonistic Behavior.—Agonistic behavior (conflict between two animals; Scott 1962) was not observed by us or the South Dakota re searchers.

Human-Ferret Interactions

Ferret responses to human activities varied. When spotlighted BFFs generally oriented toward the light and vehicle, at least momen tarily. Some moved to or stayed in prairie dog burrows, some retreated into burrows for ex tended periods, and some continued their ac tivities. When BFF heads were visible out of a hole, their eyes were often turned away from the light, perhaps avoiding the direct beam. Family groups were shy in mid-July but tended to be less shy later. Juveniles seemed to be more shy in our presence than adults. One BFF spotlighted at 75 m appeared to direct an "agoniso the observer standing 5 m way. After the marking behavior, the BFF lowly to explore new burrows.

ea. This behavior was repeated twice more in different grassy areas. After that, he moved to approached to within 2 m of us in our vehicle and on one occasion walked under the truck.

When approached on foot, BFF responses again varied. During daylight they typically retreated to burrows, observed us for short periods from the hole, and then descended the burrow. However, the distance from us at which BFFs retreat to burrows varied from 10 to 100 m. Again, juveniles appeared more shy. During daylight young BFFs popped their heads out of burrows, apparently ob serving passers-by within 100 m, but re treated if the observer approached directly. One adult female was followed at 10 m on hunting forays on 14 occasions with no appar ent alteration in her behavior because of our presence. At night several individuals, both juveniles and adults, were quietly and slowly approached in the spotlight beam or with flashlights to within 5 m. BFFs were wary of us, stayed near holes, and "hissed" at us but overall seemed curious about our activities. Whereas some BFFs later retreated to bur rows, others moved slowly between burrows. BFF response to spotlighting disturbances was briefly evaluated by Campbell et al. (1985).
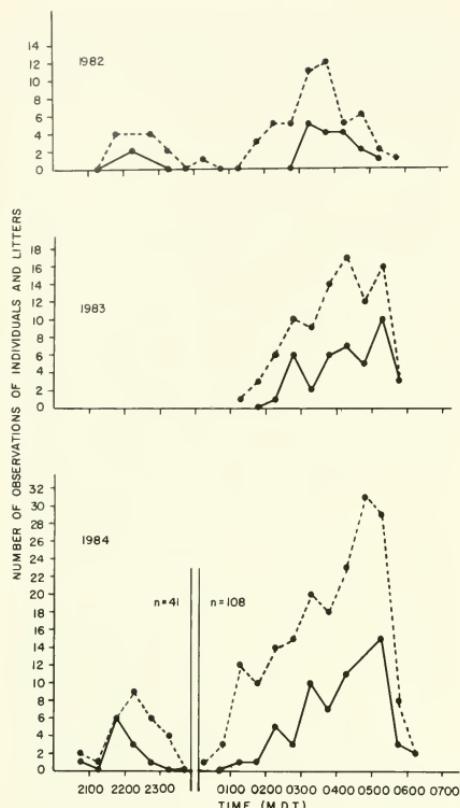
Fig. 3. Observation frequencies (by 0.5 hr intervals) for ferret litters (solid line) and single individuals and litters (dash line) on full night surveys (1982), partial night surveys (1983) (observer nights = 41), and late night surveys (1984) (observer nights = 108).

Vocalizations

BFFs emit several sounds heard by us and reported in previous studies. Based on the source and the context, we classified calls as: (1) threat, (2) defense, (3) greeting, (4) mating, and (5) sounds by young. We heard calls we labeled "bark," "huff-hiss," "growls," "ungh," and "chattering-bark." Hillman (1968) heard a "hiss," "snarl," and "bark." Henderson et al. (1969) heard an "ungh" (adult ferret to her young) and a "noise" (among young playing in a burrow). Progulske (1969) heard a "chatter" and a "low hiss." Finally, Hillman and Car- penter (1983) noted a "whimpering" (in copu- lation). Because contextual definitions are in-

complete for each call, we did not assign each call to a "functional" category.

Activity Patterns

Activity was defined as any appearance of BFFs above ground. The way in which a pop- ulation structures its activity patterns reflects its survival strategy (Orians 1961). We readily located BFFs during most months, including winter, but, like others (Hillman 1968, Hen- derson et al. 1969, Fortenbery 1972), we found that the animals themselves are easiest to locate during summer. Hillman (1968) found BFFs most active in late evening (1900–2400) and early morning (0200–0600). Frequency of BFF observation from spotlight searches conducted during July-August from 1982–1984 are shown in Figure 3.

Snowtrack evidence and direct observation showed that BFFs were active after sunrise in winter. In July BFFs were observed to be active until 1200. We watched one BFF and her litter of four for 14 consecutive mornings. She became active each morning around 0830, 2 hr after sunrise, and hunted for an hr or more. After 0930 in July, BFFs made sur- face appearances for short durations off and on until 1200 and rarely in the afternoon. Also, the same BFFs were often visible at the same hrs and in the same locations.

BFFs were active above ground in tempera- tures of -38 C, during snow and rainstorms, and in winds up to 50 kph. Richardson et al. (unpublished data) concluded that tempera- ture did affect BFF movements. Activity pat- terns of radio-tagged BFFs were described by Biggins et al. (1985).

DISCUSSION

Although the Wyoming BFF population and the one formerly in South Dakota are associated with different prairie dog species, live in different biogeographic areas, and are under different climatic regimes, much of their gross behavior and activity patterns are similar. Even though a systematic description of BFF behavior was not previously available, our categories allow for inclusion of BFF ob- servations from South Dakota. The BFF is difficult to observe, generally being nocturnal and appearing above ground at irregular in- tervals and for irregular durations. Thus, our

ethogram and activity data are incomplete, but BFF behavior apparently is similar to related species and much BFF behavior is probably homologous to other species of *Mustela*. Where behavioral data are currently lacking for BFFs (e.g., reproductive, agonistic, and ontogenetic behaviors), the most complete literature on related mustelids can be used to suggest BFF behavior patterns until observational data for the rare BFF become available. Furthermore, a comparative behavioral approach, as discussed by Eibl-Eibesfeldt (1970) and previously elucidated by Remane (1952), allows identification of homologous behavior patterns if they occur in a large number of closely related species.

Steppe ferrets live in large ground squirrel (suslik; *Spermophilus* spp.) colonies, similar to prairie dog colonies, but, in contrast to BFFs, distinctive deposition of excavated subsoil by steppe ferrets is not mentioned in the literature even though steppe ferrets do dig out susliks in winter (Stroganov 1969).

Feces and urine are deposited by BFFs as waste products but may also serve in "scent marking" (Macdonald 1980). Currently it is impossible to distinguish between feces and urine as elimination products or scent marks (see Wells and Bekoff 1981).

Steppe ferrets and BFFs hunt similarly (this study, Hillman 1968, Henderson et al. 1969). Killing methods of *M. frenata*, *M. erminea*, *M. rixosa*, *M. vison*, and *M. putorius* are basically similar (Iwen 1958). Predatory behavior of *M. nivalis*, *M. erminea*, and *M. putorius* is similar, especially for the two weasels (Gossow 1970). The killing procedure for *M. nivalis* is generally very rapid, ranging from 10 to 60 sec (Heidt 1970). Ewer (1973) characterized all mustelids as solitary, opportunistic predators whose hunting behaviors include a "random search" foraging pattern and a neck bite for killing.

The lack of "aggressive" behavior by the male BFF during copulation was unlike that for *M. eversmanni* and *M. putorius* (Hillman and Carpenter 1983). Other mustelid species display a copulatory pattern similar to that described for BFFs (e.g., Wright 1948, for *M. frenata;* Hartman 1964, for *M. nivalis*; and Rowe-Rowe 1977, for *Ictonyx striatus* and *Poecilogale albinucha*). The timing of BFF reproductive activity, as suggested by our ob-

servations, corresponds well with observations of Henderson et al. (1969) and Hillman and Carpenter (1983) for the BFF and is similar to the seasonality of reproductive activity for *M. putorius* (Walton 1976, Danilov and Rusakov 1969).

BFF growth curves, unknown at present, may be estimated based on limited data for the steppe ferret (Sviridenko 1935), our limited observations, data from the South Dakota ferret studies (Henderson et al. 1969), and from other mustelid studies (e.g., East and Lockie 1964, 1965).

Young of several mustelid species perform certain behaviors in play that probably serve them in predatory and other behaviors as adults (Gassow 1970). Play by *P. albinucha* and *I. striatus* was mainly aggressive, involving actions typical of adult fighting, prey capture, and killing (Rowe-Rowe 1977). The aggressive play of *M. putorius* appears similar to our observations and those of BFF in South Dakota. *Mustela putorius* young exhibited all three types of play (Poole 1970) that we described for *M. nigripes*. BFF play probably contains many of the motor components exhibited by adults in agonistic and reproductive behaviors, but because of the secretive, solitary, nocturnal habits of free-living BFFs, these motor patterns in an adult context are virtually impossible to observe.

The stiff-legged dance we described for young BFFs corresponds to similar behavior in *M. nivalis* (Heidt 1970) and in *Martes* spp. (Schmidt 1943), in which cases the behavior pattern was thought to be agonistic. Agonistic behavior has been extensively studied in *M. erminea* (Erlinge 1977), *M. putorius,* and *M. furo* (Poole 1966, 1967, 1972a,b, 1973, 1974) and provides descriptions that may be similar to BFFs. Our listing of vocalizations for BFFs and those from South Dakota are generally comparable to vocalizations for other mustelids (Gossow 1970, Huff and Price 1968, Svendsen 1976, Goethe 1974, Channing and Rowe-Rowe 1977, Belan et al. 1978).

Daily and seasonal activity for the Wyoming BFFs varied somewhat from that for South Dakota BFFs. Time allocation by a species reflects differences in habitat and social organization (e.g., Greenlaw 1969, Post and Baulu 1978). Our data on tracks, scats, and activity patterns have implications for conducting

BFF surveys, which are discussed elsewhere (Clark et al. *Handbook of methods*, 1984). We sought to minimize our direct contact with BFFs to reduce research impacts. Even though our data adds to an understanding of BFFs, much yet remains to be learned, including more complete behavioral descriptions and quantification of our ethogram. But, as noted by Marler (1968), the building up of descriptions is itself a quantitative process and an essential first step in revealing the behavior and ecology of a species.

Appendix

Photographs of black-footed ferrets illustrating various behaviors and ferret signs.

A. Adult female ferret and young male in alert (by Tim Clark).

B. Ferret walking (by Doug Brown).

C. Adult female in alert (by Tim Clark).

D. Adult female with prairie dog she just killed (by Tim Clark).

E. Adult female in alert (note tick in ear) (by Tim Clark).

F. Adult female emerging from burrow with just-killed prairie dog (by Tim Clark).

G. Adult female with prey—prairie dog (by Tim Clark).

H. Adult female with prey—prairie dog (not a throat bite) (by Tim Clark).

I. Juvenile ferret alert in prairie dog hole (by Tim Clark).

J. Adult ferret hunting prairie dogs (by Tim Clark).

K. Ferret dragging dead prairie dog back to her natal burrow containing some of her young (by Tim Clark).

L. Alert ferret (by Tim Clark).

M. Ferret snow marking. Tracks in photo indicate a ferret scraped or scratched through the snow into the substrate in a circular area (foreground about 25 cm diameter), made a trough in the snow with its body, and rubbed its body over and through the small shrub in background. Considered a scent-marking behavior (by Tim Clark).

N. Ferret snow marking and dirt scrape. Tracks indicate that a ferret entered the prairie dog burrow (hole diameter 10 cm), excavated a small amount of subsoil onto the snow (dirt scrape), and moved 0.3 m away from the burrow where it scraped or scratched through the snow within a roughly circular area, probably a scent-marking behavior. Note ferret tracks exiting upper left (by Louise Richardson).

0. A type of ferret digging. A ferret excavated subsoil from within a prairie dog burrow. Ferrets pull dirt out of the burrow holding it against their chests with their forepaws as they move backward, depositing the dirt in a linear fashion away from the burrow opening and sometimes making a distinctive trough or "trench" within the excavated subsoil. Digging length is about 1.5 m (by Tim Clark).

P. A ferret rubbed its body over and through the shrub in foreground (shrub about 22 cm high and 30 cm wide), with ferret tracks evident around the base of the shrub. Behind the shrub and to the right is a patch where the ferret scraped or scratched through the snow into the substrate (snow marking about 20 cm in diameter). Both markings are probably scent marking (by Louise Richardson).

Q. A ferret kill drag. Ferret entered burrow (dark area in foreground about 50 cm in diameter) from right (note dual print tracks), apparently killed a prairie dog in the burrow, and dragged it out and away from the burrow with tracks exiting to the left. The trough like depression (about 18 cm wide) was from the prairie dog's body being drug in the snow by the ferret, whose tracks are seen along the left side of the slide marks (by Tim Clark).

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ACTIVITY OF RADIO-TAGGED BLACK-FOOTED FERRETS

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Abstract. —Activity of two radio-tagged black-footed ferrets (*Mustela nigripes*) was investigated during October-November 1981 (an adult male monitored for 16 days), and during August-November 1982 (a young female monitored for 101 days). Aboveground activity of the male averaged 2.95 hr/night, 15% of the total time monitored. From 22 September to 5 November, aboveground activity of the female averaged 1.9 hours; 26% of the time she was stationary and 74% of the time she was moving. During August the juvenile female emerged at least once on 93% of the nights. She was least active in November. Both animals were primarily nocturnal (although daylight activity was not uncommon), and timing of nightly activity was similar, peaking from 0100 to 0359.

The discovery of a population of black-footed ferrets near Meeteetse, Wyoming, in 1981 (Schroeder and Martin 1982), provided an opportunity to investigate the behavior of this rare animal. We collected activity data on an adult male ferret radio-monitored during fall 1981, and a juvenile female ferret radio-monitored during late summer and fall of 1982. Spatial aspects of the activity of these two ferrets were summarized by Biggins et al. (1985); this paper addresses temporal elements of activity.

The timing of ferret activity and attendant causes has intrinsic value; however, the topic is also critical to refining spotlighting as a tool in ferret research and management (Campbell et al. 1985). Spotlighting success can be improved by knowing the time of year and time of night when ferrets are most active. Our small sample provides the first quantitative assessment of wild black-footed ferret time-activity patterns using radio telemetry.

STUDY AREA AND METHODS

Black-footed ferrets occur on a 3000 ha complex of white-tailed prairie dog (*Cynomys leucurus*) towns near Meeteetse, Wyoming. The site is a short-grass prairie at elevations ranging from 2000 to 2300 m. Vegetation and other site characteristics are described by Collins and Lichvar (1986) and Clark et al. (*Description and history*, 1986).

Ferrets were captured in Sheets' (1972) cylindrical trap and immobilized with ke-

tamine hydrochloride. Animals were fitted with a 15–g transmitter collar and allowed to recover fully from anesthesia before release. Descriptions have been given of trapping and handling procedures (Thorne et al. 1985) and of development of the transmitter packages (Fagerstone et al. 1985). Ferrets were radio-tracked from 30 October to 14 November 1981 (the male) and from 13 August to 30 November 1982 (the female). Telemetry monitoring was continuous during 16 October–5 November 1982; for other periods monitoring was mostly during the hours of darkness. Radio-tracking in 1981 consisted primarily of simple signal-following with hand-held Yagi antennas. We recorded time the male ferret spent above and below ground, but we did not attempt to separate aboveground activity into "moving" or "stationary" categories. Hand-held antennas were again employed in 1982, but most radio-tracking involved triangulation from pairs of mobile tracking stations (Biggins et al. 1985). The refined techniques and equipment allowed three types of signal status (involving strength and constancy of direction) to be telemetrically correlated with different activities: (1) changes in bearing indicated that the animal was moving aboveground, (2) consistent bearings with audible signal indicated that an animal was near or on the surface but relatively stationary, and (3) sudden loss of signal usually occurred when the animal went underground. We were able to describe daily

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and seasonal changes in activity of the female from the 101 days of monitoring in 1982; however, the limited detail and short (16–day) radio-tracking period made the data on the male best suited for only general comparisons with the female.

To avoid semantic confusion, we developed the following definitions:

period = a seasonal time category, measured in days, resulting from subdivision of the year.

interval — a time category, measured in minutes or hours, resulting from subdivision of the day.

bout of activity = a session of ferret activity occurring aboveground (or mostly aboveground), lasting >20 min and separated from other such bouts by ≥ 1 hr.

Data were summarized by tabulating presence or absence of received signal in time intervals. For overall seasonal analysis of ac tivity data on the female, a day was divided into 48 0.5–hr intervals. For each interval, the following questions were asked and positive responses recorded: (1) Was the animal telemetrically monitored during this period? (2)Was the signal absent during any part of the period? (3) Was the signal present during any part of the period? (4) Was the animal moving during any part of the period? (5) Was the animal stationary for at least part of the time? With this approach, it was possible (but un common) to have each category of activity present in a single monitoring period. Therefore, the resulting frequency data is not additive between categories; e.g., the total number of intervals with audible signal is usually not the sum of intervals containing movement and intervals containing stationary activity.

Relative importance of stationary and movement activity for the female ferret was determined by contingency table analysis using four rows of seasonal periods and two columns that represented the number of 0.5–hr periods in which the number of days with movement exceeded the number of days with stationary activity and vice versa. Only the 21 periods from 1930 to 0600 (roughly sunset to sunrise) were included because the sample size of monitoring periods during other times of the day was too small for some seasonal periods (≥ 10 days of monitoring were deemed necessary).

The seasonal emergence times of the female were compared by splitting nights (sunset to sunrise) into equal quarters to tally emergences. For a seasonal period, length of quarters was the average amount of time between sunset and sunrise during that period divided by four, quarter length being longer later in the season. Only emergences for bouts of ac tivity as defined above were considered.

Activity for the female and male from 30 October through 13 November was compared using total minutes of aboveground activity within 3–hr intervals and for each night. When gaps in monitoring occurred in either data set, corresponding time periods were deleted from both sets. This procedure allows a comparison of two animals monitored for exactly the same time periods but during two different years. Standard Chi-square tests for goodness-of-fit, Chi-square tests of independence (contingency table analysis), and t-tests were used to evaluate statistical significance of relationships, with the rejection level established at $P = 0.05$. Times are indicated on the basis of the 24–hour clock and Mountain Standard Time (MST).

Results

General Activity Patterns of the Female Ferret

During 23 September–5 November, 39 bouts of activity by the female ferret were monitored in entirety (from first appearance of radio signal to final disappearance). The average length of a bout was 1.9 hr, and an 11.7–hr bout on 27 September was the longest. During that bout, movements oc curred only during the first and last hours and were separated by 9.7 hr of stationary time during daylight. Stationary time ranging from 0.1 to 9.7 hr often preceded movement (20 occasions) or followed movement (13 occasions). Movement composed 74% of 1,569 min of activity sampled 30 October–13 November.

Daily and Seasonal Activity Patterns of the Female Ferret

From August through mid-September, the female ferret was in transition from "a social and dependent young animal to a relatively solitary and independent individual" (Biggins et al. 1985). In October and November her behavior may have differed from that of adult
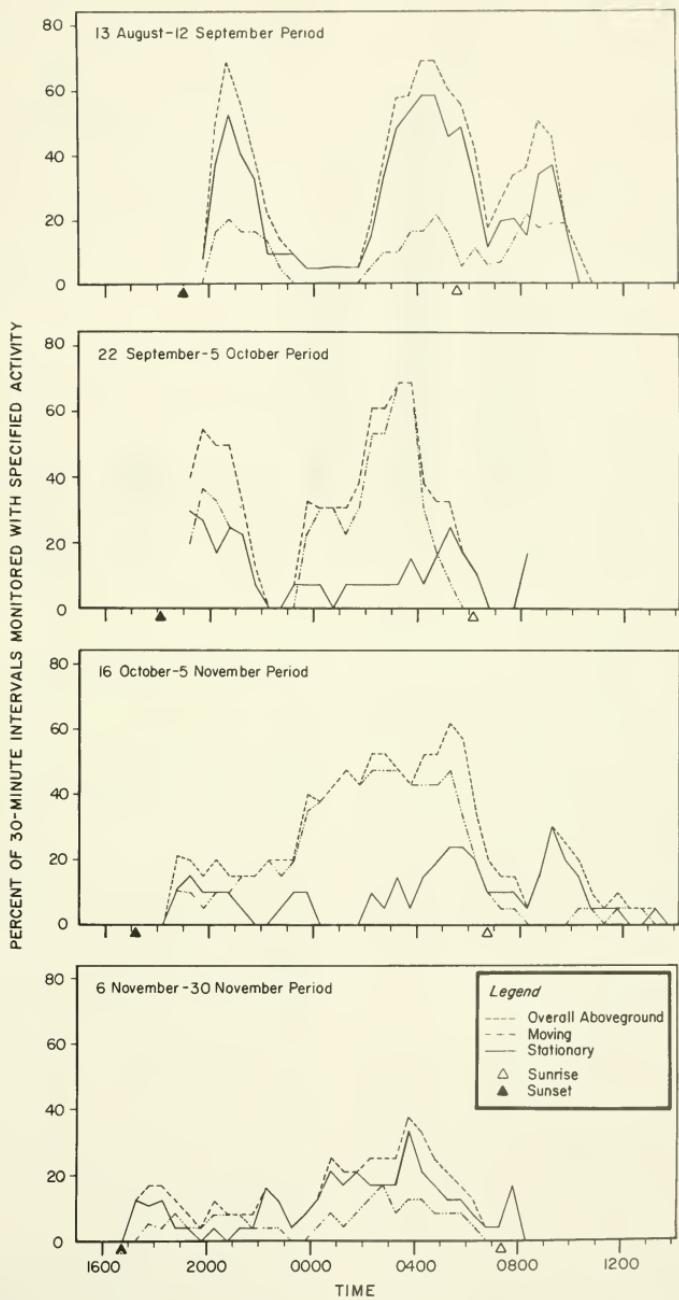
Fig. 1. Activity of a female black-footed ferret during 4 seasonal periods.

females with established home ranges and presumably better hunting skills.

The female was most active in the 13 August–12 September and 22 September–5 October periods, with $> 2/3$ of the days in five 30–min intervals containing aboveground activity. In the 6–30 November period, no 30–min interval had aboveground activity for more than 37% of the days monitored. Peaks in overall aboveground activity occurred within the four intervals from 0230 to 0429 in all four seasonal periods. The lull in all types of activity from about noon to sunset was similar to behavior of South Dakota ferrets (Hillman 1968). However, the female was active at least once during each hourly interval of day and night at some time during the study. (Activity does not appear in the noon to sunset interval on any graph because of the sample size re- striction mentioned.) Most daylight activity of the female occurred within the five hours fol- lowing sunrise. Similar behavior was ob- served in unmarked ferrets in the Meeteetse area (Clark et al. *Descriptive ethology*, 1986) and was noted in South Dakota (Hillman 1968). Morning activity was especially fre- quent during the 13 August–12 September period (Fig. 1). The female was active from 0830 to 0859 on half the days monitored dur- ing this period. The morning peak remained in the 16 October–5 November period but was delayed, perhaps due to later sunrise.

From 14 to 28 August the female (and her litter-mates) could be characterized as active and predictable. She had at least one bout of activity on 14 of 15 days (93%). She had a second bout on 8 days (53%) and a third bout on 5 days (33%,). On 11 of the 15 nights, she emerged between 1910 and 2005, shortly af- ter sunset. On 6 of the 15 nights, she emerged between 0050 and 0210 for either the first or second bout, and all five of the third bouts were in the interval 0616–0730 (at least 0.5 hr after sunrise). Over 80% (22 of 27) of all emer- gences occurred within the three intervals listed above. The prominent bimodal peaks of night activity during the period when the fe- male was part of a litter (Fig. 1) progressively changed to a more uniform distribution of activity by November. Hillman (1968) and Clark et al. (*Descriptive ethology*, 1986) also found a bimodal distribution in ferret activity, but timing differed. Comparison with these data is difficult, because Hillman's (1968)

summary covered the entire period from April through November and the information of Clark et al. (*Descriptive ethology*, 1986) covered July-August.

As implied by the seasonal depictions of activity (Fig. 1), emergence times for bouts of activity were not equally distributed through the night. When nights were split into quar- ters, significant departures from equal num- bers of emergences each quarter were noted in two of the four seasonal periods (Chi-square goodness-of-fit, d.f. = 3; 13 August–12 Sep- tember, $X^2 = 13.45$, $P = 0.004$; 22 Septem- ber–5 October, $X^2 = 5.78$, $P = 0.123$; 16 October–5 November, $X^2 = 2.429$, $P = 0.488$; 6–30 November, $X^2 = 11.35$, $P = 0.010$). The female emerged more than expected in the first and third quarters during the 13 Au- gust–12 September periods, and in the 6–30 November period she emerged more in the third quarter than in the other three quarters combined (13 of 23 times). Seasonal changes in proportions of emergences in each quarter of the night were also significant (4 season by 4 quarter contingency table, $X^2 = 23.71$, $P = 0.005$).

Relative amounts of stationary and moving types of activity changed with seasonal pro- gression and maturity of the female. She tended to make short movements or no move- ment late in the summer (13 August–12 Sep- tember)(Fig. 1). This phenomenon again ap- peared in late fall (6–30 November), but at that time of year all types of activity were infrequent. The shift in importance of move- ment versus stationary time is reflected by the seasonal change in frequency of each in the 21 0.5–hr time intervals from 1930 to 0600. Movement activity peaked during the 16 Oc- tober–5 November period when frequency of movement exceeded the frequency of station- ary activity for 18 of 21 time intervals. The decrease in movements during the next pe- riod was dramatic; only 4 of 21 intervals had higher movement frequencies. The overall seasonal change in relative amounts of move- ment and stationary activity was highly signifi- cant (4 season by 2 activity contingency table, $X^2 = 37.68$, $P < 0.0001$).

Ferrets appeared to be relatively inactive during 6–30 November 1982. Few observa- tions of ferrets were made during spotlight surveys, and little ferret sign (diggings or
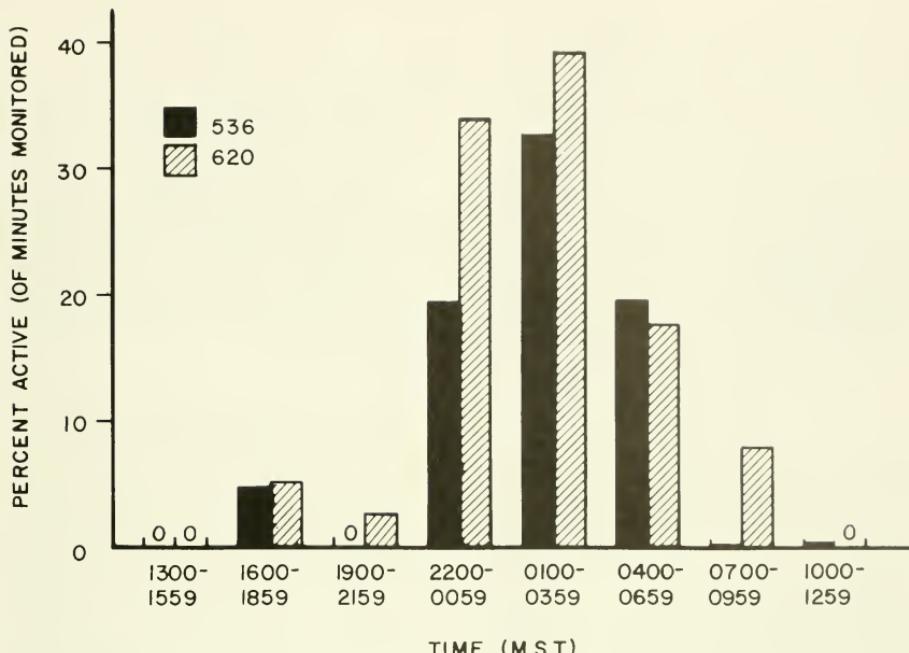
Fig. 2. Total aboveground activity of a female (No. 536) and a male (No. 620) black-footed ferret, 30 October-13 November.

tracks on snow) could be found. The radio-tagged female did not emerge during hours of darkness for 5 consecutive nights in mid-November.

Comparison of the Male and Female Ferrets

From 30 October to 13 November, daily activity patterns of the two ferrets were similar (Fig. 2). Neither animal was active from 1300 to 1559, both animals had a small amount of activity near sunset followed by decreased activity from 1900 to 2159, and both animals reached peak activity from 0100 to 0359. During 14,318 min of monitoring on each animal, the signals from the female and male were audible for 1,569 min (11%) and 2,125 min (15%), respectively. Average amounts of total time spent aboveground nightly were 2.10 hr for the female (range 0–5.79 hr) and 2.95 hr for the male (range 0–4.84 hr). These figures and the patterns illustrated in Figure 2 suggested that the adult male was more active than the young female, but we could not detect a significant difference in average nightly

activity (t = 1.044, P = 0.308). Durations of nightly activity of the female were mostly short; half were < 0.75 hours, with no activity on 3 of the 12 nights. There were 3 nights with > 5 hours of activity. In contrast, the male was never active for > 4.84 hours and was completely inactive for only 1 night; he accumulated 3.24–4.84 hours of activity on 7 of the 12 nights monitored.

DISCUSSION

Few general conclusions can be derived from the comparisons between these two animals, because data came from a different year for each animal, sexes and ages were different, and 12 nights is a small sample. However, we can hypothesize that male ferrets are more active than females. This hypothesis is consistent with comparisons of spatial activity of these two animals; the area of activity of the male was more than twice as large as that of the female (Biggins et al. 1985). Males of other small mustelid species also use larger areas

than females, based on information about stoats (*Mustela erminea*) (Erlinge 1977, Simms 1979), feral domestic ferrets (*M. furo*) (Moors and Lavers 1981), and weasels (*M. nivalis* and *M. erminea*)(Lockie 1966).

Our preliminary study has provided detailed information on only one animal during four months, and on a second animal for a much briefer period. The descriptive statistics were compiled to emphasize some behaviors detected in this species. We do not know whether these examples typify ferret activity in general, although our data support certain observations of others (Hillman 1968, Clark et al. *Descriptive ethology*, 1986). Abundance and activity of prey, breeding activity, and weather may influence ferret activity. Richardson (personal communication) found a positive correlation between temperature and movements of snow-tracked ferrets and found increased movements during the breeding season.

Seasonal changes observed in the radio-tagged female ferret imply that procedures used to locate ferrets (e.g., spotlighting) may not be generalized throughout the year. Our data suggest that the best time of night to conduct spotlight searches for ferrets from August through mid-October is from 0200 (MST) until dawn. This agrees with information collected by Clark et al. (*Descriptive ethology*, 1986) on activity of ferret litter groups in summer. Future analyses of more recent telemetric data may help identify causes of seasonal changes in activity.

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FECAL BILE ACIDS OF BLACK-FOOTED FERRETS

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ABSTRACT.—Fecal bile acid characteristics have been used to identify scats to species of origin. Fecal bile acids in scats from 20 known black-footed ferrets (*Mustela nigripes*), 7 other known small carnivores, and 72 of unknown origin were analyzed to determine if this procedure could be used as a tool to verify ferret presence in an area. Seventeen ferret scats were suitable for analysis and had a mean fecal bile acid index of 156 ± 9. This was significantly different from mean indices for the other carnivores; however, substantial overlap among confidence intervals occurred for badgers, kit foxes, and especially long-tailed weasels. We conclude this method is not useful for making positive identifications of individual ferret scats and suggest that we may be able to definitively identify individual scats with reasonable confidence by using gas-liquid chromatography.

A major research goal of the Meeteetse, Wyoming, black-footed ferret (*Mustela nigripes*) (BFF) studies is development of survey techniques (Clark 1984). From 1981 to 1984, 92 scats, 20 of known BFF origin and 72 of unknown origin but similar in size, shape, and color to known BFF scats, were collected (BFF scats pictured on p. 20 in Clark et al. *Handbook of methods*, 1984). Fecal bile acid analyses have been used to identify scats (Major et al. 1980, Johnson et al. 1984). Analysis may be performed by thin-layer (TLC) or gas-liquid (GLC) chromatography (Johnson et al. 1984). Although the latter method is more quantitative, it is also much more time consuming and expensive than TLC and requires additional training. Costs for routine management applications would probably be pro- hibitive for most government fish and wildlife agencies, especially if analyses are needed for a large collection of scats. TLC can be per- formed in less time, and several samples can be analyzed at the same time. Initial equip- ment expense for TLC is about 20% of cost for GLC. The purpose of this study was to deter- mine if thin-layer chromatographic analyses of fecal bile acids could be used as a means to positively identify scats from BFFs and thereby provide a new tool to determine BFF presence in an area.

METHODS

Scats from 20 BFFs were obtained from live-trapped specimens; they were collected along tracks of ferrets in snow (Clark et al. *Handbook of methods*, 1984; Clark et al. *Seasonality of black-footed ferret diggings*, 1984) or after field observers saw animals defecate. Another 72 scats each were collected from uncertain identity from the same area where field personnel collected the known BFF scats. To cover the range of size of the uniden- tified scats, 5 or 10 known scats each were collected from seven additional carnivore spe- cies that may frequent prairie dog (*Cynomys* sp.) colonies (Clark et al. 1982) 1979–1984: badgers (*Taxidea taxus*), long-tailed weasels (*Mustela frenata*), mink (*M. vison*), kit fox (*Vulpes macrotis*), striped skunk (*Mephitis mephitis*), red fox (*Vulpes vulpes*), and gray fox (*Urocyon cinereoargenteus*).

All scats were analyzed according to the thin-layer chromatographic method (TLC) described by Major et al. (1980). Visualization of steroid bands on TLC plates was accom- plished by spraying with 8–hydroxy-1,3,6– pyrenetrisulfonic acid trisodium salt (5 mg in 100 ml of methanol). This reagent was used in lieu of that used by Major et al. (1980) because it does not destroy the steroids. After visual- ization, locations of all steroid bands were recorded relative to the solvent front (rf). Only bands that occurred between rf values of 15% and 75% of the solvent front were consid-

ered to be fecal bile acids. Cholic and lithocholic acids are present in most species scats and usually travel at least 15% and 75% of the solvent front, respectively, using this technique (Major et al. 1980). Bile acids can be eluted from this silica gel and used for future GLC analyses.

Because there is variation in fecal bile acid concentration, we categorized scats that had less than three distinct bile acid bands as unidentifiable. This decision was justified be cause scats from no species previously described other than mountain lion (*Felis concolor*) have had fewer than three detectable fecal bile acids on TLC plates (Major et al. 1980, Johnson et al. 1981, Johnson and Aldred 1981, Johnson et al. 1984). Fresh scats from known specimens do not usually produce low quantities of fecal bile acids. However, weathered scats may, because bile acids are highly soluble in water. An average fecal bile acid index was obtained for each species by sum ming rf values for all bands in each scat and averaging among scats. Statistical analyses were performed by comparison of mean in dices among species. Data herein are means and standard errors.

RESULTS

Comparison of Known Scats

The number of bile acid bands and index means varied among the eight carnivore spe cies. Of 20 BFF scats, three contained fewer than three bile acid bands, seven had three bands, three had four bands, six had five bands, and one had six bands on TLC plates. The mean fecal bile acid index for BFF scats with three or more bands was $156 + 9$ (Table 1).

For the other seven carnivores, the number of TLC bands ranged from three to seven. Striped skunk, gray fox, and red fox scats never produced more than three bands; index means were 96 ± 1, 93 ± 3, 94 ± 2, respectively, and were significantly smaller than the BFF index ($P < .05$). The 80% confidence intervals for these species compared to those for BFFs suggested that their scats would probably not be confused with BFF scats by TLC analysis (Table 1). The mean index for mink scats (78 ± 4), which had three or four

bands, was also significantly smaller than the mean for BFFs ($P < .05$), and 80% confidence intervals did not overlap.

Mean fecal bile acid indices for badgers (179 $\pm$ 22), long-tailed weasels (197 ± 16), and kit fox (243 ± 17) were significantly larger than the mean for BFF scats at the 0.05 level of probability for type I error. However, there was substantial overlap among confidence in tervals between each of these species and BFF scats.

Regarding this overlap, less than 1% of BFF scats having an index less than 153 would be confused with kit fox scats, and less than 5% would be confused with long-tailed weasel scats. For BFF scats with an index less than 163, less than 10% would be confused with long-tailed weasel scats. Variation in fecal bile acid indices from badger scats was so large that they could not be distinguished from BFF indices. Badger scats can often be differ entiated by size from BFF scats; however, size overlap does sometimes occur, which is a problem for visual analysis.

Ten (50%) of the BFF scats produced at least three bands on TLC plates and produced in dices less than 163; nine (45%) of these were less than 153. Only four (20%) BFF scats pro duced fecal bile acid indices that were less than 163 and within the 99% confidence inter val for BFFs. Three of these scats produced indices that were less than 153.

About 35% of the BFF indices were too large to be distinguished from indices from kit fox or long-tailed weasel scats using TLC anal ysis. We estimate a 15% probability of identi fying a BFF scat with 99% confidence that it is not from a kit fox. A 15% probability exists of identifying that a BFF scat is not from a long tailed weasel with 95% confidence; or only a 20% probability of identification with 90% confidence.

In addition to the problem of misclassifying BFF scats, long-tailed weasel scats can be misclassified as BFF scats. No kit fox scats produced indices within the 80% or 99% con fidence intervals for BFF indices, so this would be an improbable source of error. How ever, 40% of long-tailed weasel scats pro duced indices that were within the 99% and 80% confidence intervals for BFF scats, thus creating a significant problem with this analy sis. The other 60% (three of five) long-tailed

TABLE 1. Mean fecal bile acid indices and confidence intervals for scats from seven carnivore species with at least three detected steroid bands between rf 15–70 on 20-cm silica gel G TLC plates.

Species	N	Mean ± SE	Confidence intervals			
			99%	95%	90%	80%
Black-footed ferret	17	156 ± 9	129–183	137–176	140–173	144–169
Badger	5	179 ± 22	69–274	109–233	123–219	131–211
Long-tailed weasel	5	197 ± 16	124–271	153–242	163–232	173–222
Kit fox	5	242 ± 17	166–321	196–290	207–280	218–269
Mink	10	78 ± 4	65– 91	69– 87	71– 85	72– 84
Striped skunk	10	96 ± 1	93– 99	94– 98	94– 98	95– 97
Gray fox	10	93 ± 3	83–103	86–100	88– 98	89– 97
Red fox	10	94 ± 2	87–101	89– 99	90– 98	91– 97

weasel scats produced indices larger than those within the 99% confidence interval for BFFs.

Identifying Unknown Scats

For the 72 unidentified scats from areas known to have BFFs, 14 produced indices less than 163, and 8 of these were within the 99% confidence intervals for BFFs and long-tailed weasels. Only 2 of the 8 scats produced in- dices below 153. We are confident that these scats were from BFFs because they were much smaller than most badger scats, were associated with apparent BFF sign, and had indices (both 138) outside the 99% confidence intervals for species other than long-tailed weasels. They were probably not from long- tailed weasels because the smallest weasel in- dex we obtained was 158. We recognize that this is the weakest point in our data because of the small number of known long-tailed weasel scats examined.

There were 12 other scats that produced indices within the 99% confidence interval for BFFs, but these indices were higher than the mean and could not be distinguished from indices for kit fox, long-tailed weasel, or bad- ger. This analysis suggests that to be reason- ably certain that BFFs are present in any area, some of the scats must produce fecal bile acid indices between 129 and 153. Only 15% (3 of 20) of bona fide BFF scats produced indices in this range. Therefore, there is a relatively large probability of not detecting BFF pres- ence when few scats are examined.

Although we estimated that about 36% (26/ 72) of the unidentified scats were likely BFF scats, only about 3% (two/72) of these scats were within the 95% confidence interval for BFFs. Assuming that no long-tailed weasel

scats will produce a fecal bile acid index less than 153, then a rough estimate for the num- ber of the 72 scats that actually were BFF scats is 13 ($2 \div 0.15$).

DISCUSSION

Although sample sizes were relatively small, this analysis suggests that the TLC method is not useful for making positive iden- tifications of individual BFF scats. Because of variation among fecal bile acid indices for BFFs and other carnivores, an individual scat could not be positively identified even though mean fecal bile acid indices were significantly different among the species. Differentiation of long-tailed weasel, small badger, and BFF scats is the most significant problem identified by our analysis.

Because about 15% of known BFF scats seemed to produce index values distinctly dif- ferent from those produced by other carni- vores, it may be possible to establish a high probability of BFF presence using indices from a relatively large collection of scats. However, whether or not this can be done depends on obtaining a better description of variation in indices produced by scats of other species, particularly long-tailed weasels and to some extent badgers. More known scats must be analyzed to improve our data base.

The differences found in fecal bile index means suggests that a more definitive type of analysis might provide a bona fide technique that can be used to identify individual scats with reasonable confidence. Recently John- son et al. (1984) demonstrated that gas-liquid chromatography (GLC) provided a more definitive distinction between fecal bile acids of bobcat (*Felis rufus*) and mountain lion than

TLC. We suggest that additional effort be ex- pended to obtain gas-liquid chromatographs as a method for identifying BFF scats. Although GLC costs are very high compared to TLC, new developments in equipment and methods will probably reduce costs substantially in the fu- ture.

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ESTIMATING GENETIC VARIATION IN THE BLACK-FOOTED FERRET— A FIRST ATTEMPT

C. William Kilpatrick[1], Steven C. Forrest[2], and Tim W. Clark[3]

Abstract.—No genetic variation was observed for three proteins examined from samples of saliva from 22 black-footed ferrets (*Mustela nigripes*). The comparable data concerning levels of genetic variation in other taxa at these loci are too inconclusive to provide a meaningful interpretation of the observed absence of genetic variation. The absence of genetic variation observed in the black-footed ferret population is compatible with the reported levels of genetic variation in terrestrial carnivores and populations that have undergone bottlenecks. Suggestions for additional studies using different approaches both to increase the number of loci that are used to determine the level of genetic variability in the black-footed ferret and to provide a more meaningful comparative data base are provided.

The importance of genetics in the management and conservation of endangered species has been recently discussed (Soulé and Wilcox 1980, Frankel and Soulé 1981, Schonewald-Cox et al. 1983). Although the primary objective of conservation and management is the continued reproduction of the species, maintenance of genetic variability has also been identified as a high priority (Benirschke 1977, Chesser et al. 1980). Without maintenance of genetic variability, the species may have an increased probability of extinction in future variable environments (Wright 1951).

The objective of this study was to obtain an estimate of the level of genetic variability present in a population of the endangered black-footed ferret (BFF) near Meeteetse, Wyoming. Salivary samples were easily taken and did not affect the survivorship of individuals sampled. Comparison of the genetic variation observed in the Meeteetse population with reported values in the literature on other species were made to determine the potential effect of the recent history of population size (bottlenecks) and isolation.

METHODS

Salivary samples were collected from immobilized animals in the field during 1982 and 1983 by swabbing the oral and buccal cavities with a cotton swab or a small piece of gauze.

Samples were frozen and shipped on dry ice to the University of Vermont for analysis of electrophoretic variation of salivary proteins.

Salivary proteins were washed from the cotton or gauze with 1–2 ml of distilled water. The residual protein solution was removed from the cotton or gauze by centrifugation at 600–800 rpm. A corner of the cotton or gauze was held outside a 15-ml screw cap centrifuge tube before placing the cap on the tube to separate the cotton or gauze from the liquid during centrifugation. Samples were frozen at -75 C until analysis.

Prior to electrophoresis, salivary samples were concentrated by the use of acrylamide sticks (Curtain 1964, Balakrishnan and Ashton 1974). Salivary amylase (AMY) was examined by the methods of Aquadro and Patton (1980), except the sample was increased to 25 μl per slot and the gel with the starch overlay was incubated overnight at 37 C before staining. Salivary esterase (EST-S) was examined by the methods of Tan (1976) except n-propanol was deleted from the stain. The method of Tan and Teng (1979) was usable for superoxide dismutase (SOD). Better results were obtained with a 10% acrylamide gel using the 8.9 tris-borate-EDTA buffer system of Coyne and Felton (1977) and with a stain of 100 ml of SOD incubation buffer (Tan and Teng 1979), 30 mg MTT, 30 mg nitro blue tetrazolium, and 2 mg phenazine methosulfate. In addition, the methods of Tan and Ashton (1976a)

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TABLE 1. Genetic variability (heterozygosity) among terrestrial mammals in which two or more of the proteins examined from the saliva of black-footed ferrets have been reported. References in parentheses are cited below; data for *Herpestes auropunctatus* are unpublished (D. B. Hoagland, personal communication).

Taxa	AMY	EST	SOD	$\bar{H}^*$	$\bar{H}^{**}$
Homo sapiens	0.138(1)	0.495(4)	0.009(5)	0.214	0.067(12)
Peromyscus maniculatus	0.315(2)		0.000(6,7)	0.158	0.122(6,7,13,14,15)
Peromyscus leucopus	0.185(2)		0.241(8)	0.213	0.081(7,8,16,17)
Mus musculus	0.048(3)		0.107(9,10)	0.052	0.098(9,10)
Herpestes auropunctatus	0.000	0.000	0.000	0.000	0.037
Mustela nigripes	0.000	0.000	0.000	0.000	?
$\bar{h}$			0.020(11)		

References: (1) Merritt et al. 1973, (2) Aquadro and Patton 1980, (3) Nielsen and Sick 1975, (4) Tan 1976, (5) Beckman and Pakarinen 1973, (6) Avise et al. 1979, (7) Loudenslager 1978, (8) Price and Kennedy 1980, (9) Selander and Yang 1969, (10) Selander et al. 1969, (11) Selander 1976, (12) Harris and Hopkinson 1972, (13) Dubach 1975, (14) Aquadro and Kilpatrick 1981, (15) Smith 1981, (16) Selander et al. 1975, (17) Browne 1977.

$\bar{h}$ — mean heterozygosity of locus.

$\bar{H}^*$ — mean heterozygosity of species based on loci examined in the black-footed ferret.

$\bar{H}^{**}$ — mean heterozygosity of species.

for salivary acid phosphatase, Tan and Ashton (1976b) for hexose-6–phosphate dehydrogenase, and Tan and Teng (1979) for lactate dehydrogenase, and saliva oxidase were attempted. No reactions were observed in the BFF salivary samples with these methods.

RESULTS

No electrophoretic variation was observed among salivary samples from 22 BFFs at the loci for salivary amylase, salivary esterase, or superoxide dismutase. Based on this very small sample of loci (n=3), the mean proportion of loci polymorphic ($\bar{P}$) was 0.000 and the mean heterozygosity (H) was 0.000.

DISCUSSION

Before the absence of genetic variability observed in the proteins from saliva of the BFF may be interpreted, some comparisons are needed. Most estimates of genetic variation are based on proteins from blood, liver, kidney, and heart or other muscle; the levels of genetic variability present in loci for salivary proteins are not well known. Saliva has been examined in very few taxa, and, in most cases, only salivary amylase has been analyzed. Superoxide dismutase, which was examined from saliva from the BFF, is also expressed in the more conventional tissue sources of proteins for electrophoretic analysis and is the only locus of the three analyzed that has been examined in a large number of taxa.

The extent of genetic variation at the three loci (AMY-1, EST-S, SOD-1) examined in the BFF was estimated in other taxa by the methods of Lewontin and Hubby (1966) and Nei (1978). Few taxa could be found in the literature for which two or more of the loci had been examined for electrophoretic variation (Table 1). Only the locus for superoxide dismutase has been examined in a sufficient number of taxa of mammals to yield a reasonable estimate of the average amount of genetic variation present. Selander (1976) reported that SOD demonstrated a low mean heterozygosity ($\bar{h} = 0.020$) among 26 species of rodents.

Although the loci for nonspecific esterases are generally considered highly variable, salivary esterase variation (Table 1) has only been reported in humans (Tan 1976). This locus apparently has not been examined in other taxa, although it is highly variable in humans.

Salivary amylase has typically not been included among the proteins examined in surveys of genetic variation in mammals. The taxa of mammals for which estimates of heterozygosity are available or from which estimates can be calculated (Merritt et al. 1973, Nielsen and Sick 1975, Aquadro and Patton 1980) appear to represent taxa in which this locus is highly variable (Table 1).

Considerable variation in levels of genetic heterozygosity at the three loci was observed, ranging from high genetic heterozygosity in *Peromyscus* to no heterozygosity in *Herpestes* (Table 1). The estimates of average heterozygosity calculated from three loci (AMY-1, EST-S, SOD-1) (Table 1) are greater than the reported heterozygosity calculated from a greater number of loci in man and *Peromyscus* but lower in *Mus* and *Herpestes* (Table 1).

TABLE 2. Genetic variation among terrestrial carnivores.

Taxa	Sample size		Mean proportion of loci		Reference
	Individuals	Loci	Polymorphic per population	Heterozygous per individual	
Canidae					
Canis lupus	12	53	0.113	0.030	Fisher et al. 1976
Canis latrans	6	53	0.132	0.050	Fisher et al. 1976
Canis familiaris dingo	6	53	0.057	0.006	Fisher et al. 1976
Vulpes vulpes	282	21	0.000	0.000	Simonsen 1982
Ursidae					
Ursus americanus	56	6	0.000	0.000	Manlove et al. 1980
	35	14	0.077	0.013	Manlove et al. 1980
	64	15	0.133	0.015	Manlove et al. 1980
	52	17	0.176	0.031	Manlove et al. 1980
	52*	33	0.121	0.016	Manlove et al. 1980
			$\bar{x} = 0.097$	$\bar{x} = 0.015$	Manlove et al. 1980
Ursus maritimus	52	13	0.000	0.000	Allendorf et al. 1979
Procyonidae					
Procyon lotor	451	24	0.133	0.021	Dew and Kennedy 1980
Mustelidae					
Mustela erminea	39	21	0.000	0.000	Simonsen 1982
Mustela nivalis	13	21	0.000	0.000	Simonsen 1982
Mustela putorius	24	21	0.000	0.000	Simonsen 1982
Martes martes	2	21	0.000	0.000	Simonsen 1982
Martes foina	121	21	0.000	0.000	Simonsen 1982
Meles meles	5	21	0.000	0.000	Simonsen 1982
Felidae					
Felis catus	56	55	0.220	0.069	O'Brien 1980
Aciononyx jubatus	50	47	0.000	0.000	O'Brien et al. 1983
Herpestidae					
Herpestes auropunctatus	45	29	0.241	0.037	unpublished data
			$\bar{x} = 0.062$	$\bar{x} = 0.014$	

*Same population as above, including analysis of 16 additional loci.

If the data for humans and *Peromyscus* are typical, these three loci are highly variable and tend to give a higher estimation of genetic variation than estimates based on a larger number of loci. This would suggest that a great deal of genetic variation has been lost from the Meeteetse population of BFFs. However, the estimates of genetic variation in these taxa are based, for the most part, on reports of genetic variation at a single locus and not on surveys of a number of loci. This would appear to result in a biased data set, since loci observed to be monomorphic (invariable) are not reported unless they are part of a survey of loci.

If the data for the small Indian mongoose, *Herpestes auropunctatus*, (Table 1) are typical (or typical for carnivores), these loci demonstrate little or no genetic variation. This would suggest that these loci provide little information concerning the total levels of genetic variation present in the Meeteetse BFF population. The comparative data avail-able concerning the genetic variation at these three loci (Table 1) are inconclusive for providing a meaningful interpretation of the observed absence of genetic variation at these loci in the BFF.

Although it is important to continue attempts to determine the existence of genetic variability that could be managed in the Meeteetse BFF population, the absence of genetic variation observed thus far may be the result of a recent bottleneck or may be typical for carnivores. Some mammals that have passed through severe bottlenecks demonstrate an absence of or a very low level of heterozygosity (Bonnell and Selander 1974, Ryman et al. 1977, O'Brien et al. 1983). However, the North American bison (*Bison bison*), which has also gone through a bottleneck, has a mean heterozygosity of 0.023, and a small Indian mongoose population, which was derived from a few individuals introduced to St. Croix in 1884, presently has a level of heterozygosity of 0.037. The effect of the bot-

tleneck on the level of genetic variability is dependent upon the rate at which the population recovers from the reduced population size (Smith 1981) and not on the bottleneck alone.

Pettus (1985) suggested that carnivores and perhaps other species of large mammals are employing the Mullerian strategy and would be expected to exhibit little genetic variation. Carnivores appear to have somewhat lower levels of genetic variation (Table 2), with a mean heterozygosity of 0.014 for 16 species as compared to a mean heterozygosity for 46 species of mammals of 0.036 (Nevo 1978). No genetic variation has been observed in any of the six taxa of the family Mustelidae (Table 2) that have been examined. Unfortunately, these have been examined by only one laboratory (Simonsen 1982), and the sample sizes of some taxa were very small.

Although the mean heterozygosity observed in carnivores is below the mean value of other mammalian taxa, several species demonstrate levels of heterozygosity typical for mammals (Table 2). Those taxa that demonstrated the highest levels of genetic variation among carnivores (Table 2), *Felis catus* and *Canis latrans*, are those with estimates based on the largest number of loci. The effect of examining a small number of loci is clearly seen in the estimates of genetic variation in the American black bear (*Ursus americanus*), as pointed out by Manlove et al. (1980). The level of genetic variability in different populations increases with the number of loci examined (Table 2).

Future work should include continued research to provide an estimate of genetic variation in the Meeteetse population of BFF based on a larger number of loci. This research could include an examination of additional loci from nontraditional sources such as saliva (Tan and Teng 1979), urine (Hayakawa et al. 1983), and feces (Scribner and Warren 1984). Examination of blood samples (hemolysate and serum), however, would allow detection of genetic variation at 30 to 40 loci.

By including loci for proteins from nontraditional sources, other surveys of genetic variation in mammal taxa could provide a better understanding of levels of genetic variation present at these loci. Other surveys of genetic

variation in carnivores, especially within the mustelids, including loci for proteins from traditional and nontraditional sources, would provide a better data base from which to determine what portion of the total genetic variability could be expected to be identified from salivary samples.

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DETERMINING MINIMUM POPULATION SIZE FOR RECOVERY OF THE BLACK-FOOTED FERRET

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ABSTRACT.—A minimum viable population (MVP) size is estimated for the critically endangered black-footed ferret by examining five basic methods: experiments, biogeographic patterns, theoretical models, simulation models, and genetic considerations. Each method is evaluated for its applicability to the ferret and endangered species in general with two criteria in mind: (1) potential research impacts to target species and (2) the value of scientific accuracy and precision in relation to short-term conservation needs. For the black-footed ferret, the genetic method proved to be the most useful, resulting in an MVP estimate of about 200 ferrets for maintenance of short-term fitness. For most endangered species, a combination of the simulation and genetic methods will probably yield the best estimate of MVP size. MVP estimates have direct implications for future research, management, and recovery efforts of endangered species.

Following the 1981 discovery of the critically endangered black-footed ferret (*Mustela nigripes*) in northwestern Wyoming, the only population of the species known, two primary goals of a ferret study were established: (1) conservation of the population and (2) recovery of the species (Clark 1984a). Estimation of population parameters such as distribution, birth rate, death rate, and immigration/emigration was a major objective. In addition to providing valuable life history data for the ferret, estimating these parameters would enable us to address a key question: What is the minimum ferret population size necessary for the species to persist (i.e., avoid extinction)? Because of the apparent small size of the Wyoming population in 1981, the answer was paramount for successful conservation and, ultimately, species recovery.

The minimum population size concept for species conservation was recently introduced by Shaffer (1981), with potentially significant implications for endangered species programs. Although many endangered species studies have been conducted, few have tried to estimate minimum population sizes (Shaffer 1978, 1981, Lacava and Hughes 1984, Salwasser et al. 1984). Although USDA Forest Service regulations require that minimum viable populations of endangered species be maintained on Forest Service lands, these population numbers are not estimated but are instead routinely established as those levels specified in recovery plans

(Lacava and Hughes 1984). In this paper, we estimate minimum ferret population numbers and, as a corollary, minimum area requirements. Our purpose is to establish guidelines for future ferret research and management and to provide impetus, direction, and encouragement to other endangered species programs to use the concept of minimum population size.

CONCEPT OF MINIMUM VIABLE POPULATION SIZE

The notion of a required minimum population size for species conservation was first embodied by Shaffer (1981) in his concept of minimum viable population (MVP) size. He defined the MVP for a species as the smallest isolated population having a 99% chance of remaining extant for 1000 years despite foreseeable effects of four types of stochastic events: (1) demographic stochasticity, or the chance events in the survival and reproductive fitness of a finite number of individuals; (2) environmental stochasticity, or perturbations due to habitat parameters, competitors, predators, and disease; (3) natural catastrophes, such as randomly occurring floods, fires, droughts, etc.; and (4) genetic perturbations resulting from changes in gene frequency. Shaffer (1981) stressed the tentative nature of his definition and emphasized the importance of defining MVP with explicit but flexible criteria such as time frame and survival probability. For

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example, the survival probability could be set at 95% or any other level, and the time frame could be shortened or lengthened as appropriate for planning needs.

Shaffer (1981) proposed five basic methods for determining MVP size: experiments, biogeographic patterns, theoretical models, simulation models, and genetic considerations. In the next section, we elaborate on the application and utility of each method for estimating MVP size for ferrets in particular and endangered species in general. The usefulness of each method is pragmatically evaluated relative to: (1) acceptable levels of potential research impacts on target species and (2) the real value of scientific accuracy and precision in relation to short-term conservation needs. In endangered species recovery work, these two concerns must be addressed.

The MVP concept is a rapidly evolving one. In late 1984, the Forest Service and other agencies sponsored a workshop to provide a state-of-the-art review of the MVP issue (M. L. Shaffer, personal communication). A major purpose of the workshop was to consider revisions of Forest Service procedures for estimating MVP size. The primary focus of the workshop was a discussion of the relative importance of demographic, environmental, and genetic variability in determining minimum population numbers as well as the development of new simulation and analytical models for estimating MVP size. Proceedings of this workshop, which will be published in 1986, may provide additional methods not discussed in this paper and/or may suggest revisions of methods outlined and discussed below for estimating MVP sizes of endangered species.

DETERMINING MVP SIZE

Experiments

This method establishes isolated populations of species and monitors their population dynamics through time. If censusing can be accomplished without stressful manipulation of individuals (as can occur in a capture/recapture program), this approach requires only low levels of research activities. The only necessary data are population numbers and the area inhabited over a specific time period (i.e., time frame in MVP definition).

Determining MVP via experimental methods brings up three concerns. Although methodo-logically simple, this approach is not plausible for many species, particularly endangered ones. First, for many endangered species, there exists no possibility of studying several isolated populations. In the case of the ferret, there is only one known population, and consequently there is no way to measure variability in persistence of different-sized, isolated populations. Second, time is not an unlimited resource in most endangered species studies. The years necessary to monitor persistence of populations for MVP estimates are simply not available for most endangered species. Lastly, many wildlife species cannot be censused sufficiently without some type of mark/recapture program. These techniques can have negative research impacts (e.g., trap mortality) that some endangered species projects may not be willing to risk, particularly in the early stages. Because endangered species programs in general possess high levels of uncertainty, there may be hesitancy to increase uncertainty to even greater levels (Clark 1984b). Such has been the case in the Wyoming ferret project, where one research team chose initially not to employ mark/recapture and radio telemetry procedures until other methods proved the population large enough to withstand some stress (Clark 1981).

The experimental method could prove useful when extensive population data are available prior to a species becoming endangered. For example, mountain goat (*Oreamnos americanus*) and bighorn sheep (*Ovis canadensis*) populations have been reintroduced to several sites in the western United States in recent years (Rideout 1978, Wishart 1978). If wildlife researchers monitor the dynamics of these introduced populations, the data should eventually allow them to estimate MVP sizes for these species. Such information would be useful not only for future translocations of these species' populations but also for management if, for example, an isolated population showed a decline in numbers.

Biogeographic Patterns

By studying the distribution patterns of species occupying patchy or insular habitats, an estimate of MVP size and minimum area requirements can be obtained. However, populations examined should be in equilibrium and their approximate period of isolation known (Shaffer 1981). Under these conditions, researchers can estimate the smallest area inhabited by a species
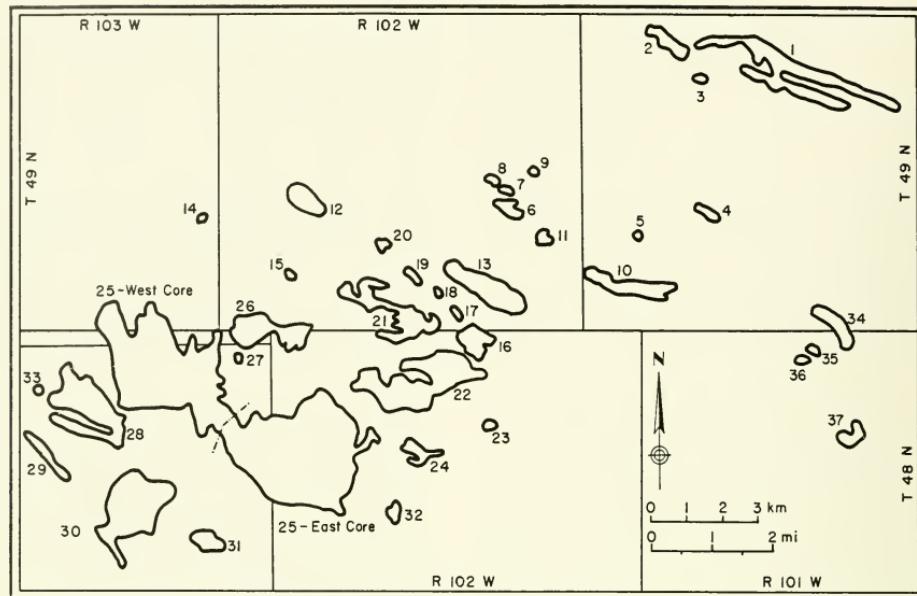
Fig. 1. Distribution of 37 white-tailed prairie dog colonies on the Wyoming black-footed ferret study area, 1981–1984.

and the percentage of patches of a particular size that a species occupies. The smallest population that has persisted over an extensive time period can then provide a first estimate of MVP size.

Because the ferret occupies a patchy habitat (i.e., prairie dog colonies with relatively discrete boundaries, Fig. 1), this approach can be applied, at least in part, to the Wyoming population. Old time trappers have reported catching ferrets in the 1920s and 1930s on the Wyoming study area, thus indicating that ferrets may have occupied the site for at least 50 years. Extinction and recolonization, although unlikely, could have occurred during this period. Population censuses over the last four years (Clark 1986) suggest that the Wyoming ferret population is not in equilibrium but is increasing. As a result, more sophisticated census techniques (e.g., mark/recapture) are being used, leading to more precise and accurate population data. In the future, researchers should thus be able to determine with some degree of confidence whether the Wyoming population is reaching an equilibrium density.

If the Wyoming ferret population stabilizes in numbers, then data from this population will provide the first field assessment of MVP size

and minimum area requirements for the species. However, due to the time required to obtain these data, the biogeographical method will not likely be useful for short-term management decisions concerning MVP size. Nevertheless, useful information on minimum area requirements can be gleaned from the biogeographical approach.

In the short run, researchers will need to decide what size of an area is necessary for ferret reintroduction or translocation for recovery planning (Forrest et al. 1985; Houston et al. 1986). A recommendation for an area larger than the Wyoming site is warranted for two reasons. First, two habitat patches (e.g., Wyoming and South Dakota) of equal size may not be the same in habitat quality. For example, Wyoming ferrets occur on white-tailed prairie dog (*Cynomys leucurus*) colonies, whereas a South Dakota population of ferrets occupied black-tailed prairie dog (*C. ludovicianus*) colonies (Hillman and Clark 1980). White-tails usually form small, sparsely populated colonies; black-tails form large, densely populated colonies (Hoogland 1981). Consequently, a habitat patch that is large enough in one part of the range of the species might be insufficient in another due to differ-

ences in habitat quality. Second, nothing is known about the frequency with which ferret populations go extinct on habitat patches of various sizes. Therefore, it would be inadvisable to rely on the size of the Wyoming study area as an exemplary model of area requirements for black-footed ferrets.

Although the biogeographical approach cannot be used for endangered species with contiguous distributions, it is applicable for species with insular or patchy distributions. Its greatest use should be for endangered species that occupy patches of different size and similar quality and for which data on population numbers and isolation periods are available. For example, the Shoshone sculpin (*Cottus greenei*) is restricted to different-sized spring systems along a 45–km stretch of the Snake River in south central Idaho (Wallace et al. 1984). Relative and absolute densities of the sculpin in many of these spring systems were determined during a status survey in 1980–1981 (J. Griffith, personal communication). By monitoring the persistence of these spring populations of this short-lived species over the next several years, researchers could estimate MVP size and minimum area requirements for this species.

Theoretical Models

Although there are several theoretical models that predict extinction probabilities and times for a population, most are too complex for the simple data bases of endangered species. The theory of island biogeography (MacArthur and Wilson 1967), however, has received considerable attention in the conservation field. Though originally developed in relation to true oceanic islands, this theory has been widely applied to continental habitat "islands" or patches (e.g., Brown 1971). The theory's greatest potential application has been in the design of nature preserves for maintenance of species diversity (for review, see Margules et al. 1982). Much less attention has been devoted to those aspects of the theory that predict the distribution of a single, insular species (Smith 1974, Fritz 1979).

Because the Wyoming ferret population is located on a large habitat "island" (i.e., prairie dog colony complex in Fig. 1), we employed the T_k model of island biogeography to predict probabilities of successful colonization and times to extinction for the ferret. Regarding the Wyoming prairie dog colony complex as a single is-

land is supported by three lines of evidence: (1) several prairie dog colonies at the Wyoming site contained at one time or another only one adult ferret, suggesting that interbreeding of ferrets among prairie dog colonies is occurring, (2) movement data reveal that ferrets range an average of 2.5 km between colonies, with the maximum intercolony movement being 5.7 km (Forrest et al. 1985), and (3) aerial and ground surveys indicate that potential ferret habitat declines significantly beyond the boundaries of this single colony complex, strongly suggesting that these ferrets represent a distinct, isolated population.

Data required in the T_k model are carrying capacity (K), per capita birth rates (λ), and per capita death rates (μ). Direct observations of ferret litters in Wyoming indicated an average litter size of 3.4, or 1.7 female young per adult female (Forrest et al., in manuscript). We assumed that the sex ratio approximated unity, natality did not vary with age, and all females bred. No data on juvenile mortality were available for ferrets; data from other mustelids indicated a medium (60%) to high (80%) rate of juvenile mortality (King 1980, *M. nivalis*; King 1983, *M. erminea*; K. C. Walton personal communication, *M. putorius*). We used a juvenile mortality rate of 0.7, resulting in a λ of 0.5. As with juvenile mortality rates, no data on adult mortality rates were available for ferrets. Data from other mustelids indicated adult mortality ranged from 15%-25% for *Martes pennanti* (Kelly 1977), *M. americana* (Strickland et al. 1982), and *Mustela erminea* (Stroganov 1937), although King (1980) reported mortality rates of 80%-90% for *M. nivalis*. We varied adult mortality (μ) for ferrets from 0.2 to 0.4.

The probability of ferret populations of size n reaching a size where the probability of extinction is nearly zero was calculated by

$$P \sim 1 - (\mu/\lambda)^n$$

where μ and λ are the per capita death and birth rates, respectively (MacArthur and Wilson 1967, Richter-Dyn and Goel 1972). Two results emerged from this analysis (Table 1). First, as μ/λ decreases, the number of female ferrets needed to colonize an area successfully decreases for a given probability. Second, as the number of breeding females increases, a higher μ/λ can still be tolerated with a high probability of successful colonization. These results have a practical application in the reintroduction of

TABLE 1. Probability of a female black-footed ferret population of size n successfully colonizing and reaching carrying capacity. For a birth rate (λ) of 0.5 and a death rate (μ) varied from 0.2 to 0.4, the resulting μ/λ ranges from 0.4 to 0.8.

Population size (n)	Death rate/birth rate ratio (μ/λ)					
	0.9	0.8	0.7	0.6	0.5	0.4
5	0.41	0.67	0.83	0.92	0.97	0.99
10	0.65	0.89	0.97	0.99		
15	0.79	0.96	0.99			
20	0.88	0.99				
30	0.96					
40	0.98					
50	0.99					

TABLE 2. Times to extinction (T_k) for black-footed ferret populations with a carrying capacity (K) of 40 and 50, and birth (λ)/ death (μ) rates varied as shown. See text for details.

	λ	μ	μ/λ	T_k (years)
$K = 40$	0.5	0.2	0.4	1.0×10^{15}
	0.5	0.3	0.6	3.0×10^{7}
	0.5	0.4	0.8	1.0×10^{3}
$K = 50$	0.5	0.2	0.4	8.0×10^{18}
	0.5	0.3	0.6	5.0×10^{9}
	0.5	0.4	0.8	5.0×10^{4}

black-footed ferrets. For example, if μ/λ is conservatively estimated to be 0.9, these data suggest that at least 15 females will be needed for a reintroduction that has an 80% chance of succeeding. As more accurate birth and death rates are estimated for the Wyoming ferrets, this type of analysis will become even more useful for assessing the number of animals needed for translocations.

We also calculated extinction times for an established population of ferrets (Table 2). These values (T_k) were estimated by the MacArthur and Wilson (1967) equations

$$T_k \sim T_1 \frac{\lambda}{\lambda - \mu} \quad \text{where}$$

$$T_1 = \sum_{i-1}^{k} (\lambda/\mu)^i \cdot (1/i\lambda)$$

As the death rate to birth rate ratio (μ/λ) increases, the time to extinction (T_k) decreases. For a given μ/λ, T_k increases as the carrying capacity (K) increases. Assuming that the carrying capacity of the Wyoming ferret population is approximately 40 adults (Forrest et al. 1985) and that μ/λ equals 0.8, the time to extinction for this population as predicted by the T_k model would be about 1,000 years. Data from Table 1 show that this population of 40 (20 females, 20 males) with a death rate/birth rate ratio of 0.8 would have about a 99% chance of successful colonization and conversely less than a 1% probability of extinction. Thus, a population of 40 adult ferrets should be a reasonable first estimate of MVP size as predicted by the T_k model. If we assume that there is a constant average density of ferrets across the study area of 1/50 ha (Forrest et al. 1985), this MVP estimate would result in a minimum area requirement of 2,000 ha. In actuality,

because prairie dog densities vary in this habitat (Clark et al. 1985), the 2,000 ha figure is low.

For endangered species with insular or patchy distributions, the theory of island biogeography can be a useful tool for estimating MVP size if data on birth and death rates are available. The T_k model is a mathematically simple one that assumes limited exponential growth, either birth or death rates that vary linearly with density, no age-specific variance of birth and death rates, and a constant environment. Nevertheless, the T_k model has at least two serious drawbacks: (1) it ignores inbreeding depression (see genetic considerations), which may be important in small populations, and (2) violation of the model assumptions decreases the time to extinction (T_k), thus producing what may be overly optimistic T_k values (Shaffer and Samson 1985). For the ferret, there is good evidence that not all females breed and that natality varies with age (Forrest et al., in manuscript), thereby violating two assumptions of the model. The degree to which these violations may decrease extinction times is unknown.

Other researchers have criticized all aspects of island biogeography theory, the T_k model included, claiming it remains essentially unsubstantiated (Gilbert 1980, Margules et al. 1982). Despite these criticisms, several studies have shown good agreement between model predictions and field observations. Crowell (1973) reported good accordance between observed and predicted times to extinction for mice introduced to islands. Similarly, Smith (1974, 1980) and Fritz (1979) predicted times to extinction that appeared to explain satisfactorily local distributions of pikas (*Ochotona princeps*) and spruce grouse (*Canachites canadensis*). We suggest that the T_k model of island biogeography remains a useful one that should be used in conjunction with other methods to estimate MVP size and area requirements.

Simulation Models

Computer simulations may be the most useful method to estimate MVP size and minimum area requirements. Except for theoretical models like the T_k of island biogeography, computer models provide the only method in which a probability value for survival can be attached to the MVP estimate. In addition, these models are not confined to the mathematical assumptions of analytical models (e.g., density dependent natality or mortality rates, lack of age structure) and provide a flexible mechanism for assessing the sensitivity of MVP estimates to changes in certain population parameters.

Shaffer (1978) employed the simulation approach to estimate MVP size and minimum area requirements for the grizzly bear (*Ursus arctos*) in Yellowstone National Park. This simulation evaluated the effects of both demographic and environmental stochasticity and also indicated which population parameters were most likely to affect changes in survival probability. Watts and Conley (1981) used both stochastic and deterministic models to predict survival and extinction probabilities for a remnant population of bighorn sheep in the southwestern United States. Their simulations evaluated the effects of demographic but not environmental stochasticity. Although an estimate of MVP size was not an explicit result of their effort, it could have been obtained from their simulations.

The major disadvantage of the simulation approach is the extensive population data it requires. Minimum data requirements are the mean and variance of age-specific and sex-specific natality/mortality rates, age structure, sex ratio, and the relationship of these variables to density (Shaffer 1981). For most species, obtaining these data requires an extensive and intensive mark/recapture and/or radio telemetry effort over several years. In his grizzly bear simulation, Shaffer (1978) used the 12–year data base of Craighead et al. (1974). Such extensive data for any wildlife species are the exception, not the rule. However, for some species in which data are lacking, it should be feasible to substitute data from a closely related (congeneric) species into the simulation.

The black-footed ferret is a case in point. Although some natality and sex ratio data are available (Forrest et al., in manuscript), mortality data are not. With ferret data on natality and steppe polecat (*M. eversmanni*) data on mortality, Shaffer (personal communication) simulated some preliminary estimates of MVP size for the ferret. Work is now in progress to refine these simulations, which will take into account both demographic and environmental stochasticity. As the Wyoming ferret study proceeds, more age- and sex-specific natality/mortality data may become available to incorporate into the simulation. For short-term management needs, however, a MVP estimate by simulation using data from a closely related species should suffice for the black-footed ferret.

Although not directly useful in estimating MVP size, simulation models based on bioenergetics are useful in estimating minimum area requirements. Two such models exist for the ferret. One model estimates gestation, lactation, and growth energy requirements for one female ferret and her young (Stromberg et al. 1983); the other estimates energy requirements based on experimental feeding studies of steppe polecats and observed activity patterns of the Wyoming ferrets (Powell et al. 1985). Both models indicate the number of prairie dogs required to support a given population of ferrets. Combined with estimates of MVP size, data from these models are helpful in estimating minimum area requirements for the ferret, assuming that prey (prairie dog) densities can be measured and that there is a close correspondence between prey density and availability.

Computer simulations, though realistic in some aspects, cannot incorporate all the behavioral and ecological adaptations of every species (Watts and Conley 1981). They should not be used to predict actual population parameters but instead should indicate a range of possibilities for those parameters (Fowler 1981). In discussing the role of computer simulations in wildlife science, Romesburg (1981) viewed these models as comprehensive tools for integrating knowledge, common sense, hunches, and opinions. It is in this role that we feel computer simulations can be an aid to estimating MVP size and minimum area requirements for endangered species. Shaffer's grizzly bear simulation is presently being used by wildlife managers in Montana and Wyoming in this capacity. In addition, an adaptation of his simulation is currently being made available to the USDA Forest Service for use in the management of vertebrate species in their forest planning process (Shaffer, personal communication).

Genetic Considerations

Increasing attention is being given to estimating minimum population numbers from a genetic standpoint (Soulé and Wilcox 1980, Frankel and Soulé 1981, Schonewald-Cox et al. 1983, Lacava and Hughes 1984, Lehmkuhl 1984, Salwasser et al. 1984). The critical question is what population thresholds are necessary to maintain short-term and long-term (evolutionary) fitness. Based on the extensive experience of animal breeders, Franklin (1980) and Soulé (1980) determined that the maximum allowable rate of inbreeding necessary to avoid short-term effects of inbreeding depression is 1% per generation. This rule of thumb translates to a genetically effective size of 50 for maintenance of short-term fitness.

The concept of a genetically effective population (N_e) is important. Such a population is defined as one in which all individuals mate randomly, the sex ratio approaches unity, variance in family size is zero, and generations do not overlap. Obviously, few if any vertebrate populations meet these criteria. Thus, a genetically effective size of 50 translates into a larger actual (census) number of breeding adults for most species.

Several mathematical expressions have been derived for determining the effects of variance in progeny, unequal sex ratios, overlapping generations, and population fluctuations on the genetically effective population size (e.g., Kimura and Crow 1963, Emigh and Pollak 1979). Lehmkuhl (1984) developed a procedure, based on the above formulae, for adjusting the genetically effective population of 50 to arrive at the census number of breeding animals. With Lehmkuhl's procedure, we estimated the number of breeding ferrets (N) necessary to maintain a genetically effective population (N_e) of 50 (see the Appendix for calculations). Results of this exercise indicated that a MVP of 214 breeding ferrets is necessary for maintenance of short-term genetic fitness. This MVP estimate is five times the known number of adults in the Wyoming population (Forrest et al., in manuscript). Minimum area requirements for this MVP estimate would be about 10,700 ha of white-tailed prairie dog habitat.

A question arises as to what constitutes short-term versus long-term genetic fitness. This question can be satisfactorily answered with the following equation

$$f = 1 - \left(1 - \frac{1}{2\,N_e}\right)^t$$

where f equals the inbreeding coefficient, N_e equals the genetically effective population size, and t equals generation time. Animal breeders have noted a significant reduction in fecundity when f approaches 0.5–0.6 (Soulé 1980). Setting N_e at 50 and f at 0.6 in the above equation results in t equal to about 90 generations. If the generation time for the ferret is 1 year (time from birth of a female kit to birth of her first litter), it would take about 90 years for an effective population of 50 ferrets to reach an inbreeding coefficient that could cause extinction solely on genetic grounds. If the N_e for the Wyoming ferret population is now substantially less than 50 animals, this short-term genetic threshold could be reached in considerably fewer than 90 years. The amount of time the population has already been isolated may be several decades.

Franklin (1980) suggested that a genetically effective population of 500 animals is necessary for long-term genetic variation required by the evolutionary process. As with short-term fitness, a N_e of 500 translates into a much larger number of breeding adults when dealing with real, as opposed to ideal, populations. As an alternative to this rule of thumb approach, Frankel and Soulé (1981) suggested monitoring genetic variation in target species by electrophoretic techniques that estimate percentage polymorphisms and percentage heterozygosity in a population. Data from natural populations suggest that relatively heterozygous individuals have greater viability and fecundity than individuals with lower percentages of heterozygosity and polymorphism (Soulé 1980).

For many species, particularly endangered ones, electrophoretic techniques can be impractical for several reasons. First, they require potentially injurious tissue sampling. Second, small sample sizes of most studies can verify the presence but not the absence of rare alleles and preclude the use of statistics to test departures from Hardy-Weinburg frequencies. Third, many higher vertebrates lack polymorphic genetic markers that these techniques can detect. Nevertheless, if these techniques become more efficient and automated in the future, they could be a valuable management tool for working with threatened and endangered species. If test results indicated a reduction in genetic variability, then restorative steps, such as increasing N_e,

could be taken (Frankel and Soulé 1981). Base-line data on genetic variation in the Wyoming ferret population are now being gathered (Kil-patrick et al., 1986).

Although both empirical data and theory have contributed to developing the genetic approach to estimating MVP size, this method is not without its shortcomings. Both the "50 and 500 rules" which are being advanced are based on simple, analytical models of population genetics that do not account for either age structure or environmental stochasticity. Previous work indicates that the exclusion of age structure can dramatically decrease MVP size (Shaffer 1978) and in so doing optimistically deflate the MVP estimates.

DISCUSSION AND CONCLUSION

At the outset of this paper, we indicated that the five methods for estimating MVP size would be evaluated in relation to research impacts on target species and the value of accurate and precise data when time is a critical factor. In the black-footed ferret study, we adopted the pragmatic philosophy of Frankel and Soulé (1981) that conservationists must often employ rough approximations of critical parameters instead of waiting for precise data that may never be obtained. Assuming that this philosophy is sound for most endangered species studies, in practice it leads us to conclude that the experimental and simulation methods for estimating MVP size have serious limitations. The former requires a lengthy study period, and the latter an extensive set of population data. Neither time nor extensive population data are goods in great supply for most endangered species programs. As previously pointed out, though, it should be possible at times to use less than "perfect" data in the simulation approach to produce a meaningful MVP estimate.

Although Shaffer (1981) underscored the importance of defining MVP size with explicit but flexible criteria (i.e., time frame and survival probability), only two of the five methods examined (T_k and simulation) yield results that include both of these criteria. Are we then to dismiss the other approaches as meaningless exercises? We think not. When applicable, both the experimental and biogeographical methods provide empirical data for estimating MVP size, although no survival probability can be attached to their estimates. A prudent path for any con-servation biologist should be to use both empirical as well as theoretical approaches such as island biogeography and genetic considerations.

Each of the methods for estimating MVP size relies on several assumptions. Which method(s) then are most appropriate? Looking at this same question from another angle, one might ask to which type of perturbation is the target species or population most susceptible. For most endangered species, it is unlikely that the latter question will be answerable; it is likely that the target species will be subject to some combination of demographic, environmental, and genetic perturbations. Therefore, those methods that take into account these perturbations should probably carry the most weight. Obviously, the available data will also dictate to some extent which methods can be used.

For the majority of endangered species studies, empirical data necessary for estimating MVP size with the experimental and bio-geographical methods will not be available. If population data on natality and mortality are obtainable, then a combination of the simulation and genetic approaches may yield the best estimate of MVP size. The simulation method can account for both demographic and environmental perturbations, and the genetic method can account for demographic stochasticity as it relates to genetic drift. On the other hand, theoretical methods like the T_k model of island biogeography only account for demographic perturbations. A combination of the simulation and genetic approaches will likely produce a range of MVP estimates. Results of the recent Forest Service workshop indicated that environmental and demographic variability may be more important than genetic variability in setting the lower limit to population viability (M. L. Shaffer, personal communication). One possible implication of these results is that the final MVP estimate should be biased toward that estimate produced by the simulation method. However, management constraints will also be a primary factor in establishing MVP size somewhere within the range of estimates.

When no population data are available and empirical approaches have also been ruled out, then genetic considerations must take priority in estimating MVP size. This is the case for the ferret. Until more data are obtained for simulations, we must rely on our estimate of about 200

animals by the genetics method to serve as the MVP estimate for black-footed ferrets. In the final analysis, this number may be reduced as a result of compromising between estimates from the simulation and genetics methods.

The preceding discussion on genetic ap proaches is relevant only to maintenance of short-term fitness. For fitness on a long-term scale, we must try to establish several ferret populations, each of which maintains a short term MVP size. Although such goals may now appear beyond the vision of what resource managers can do to conserve the ferrets in the near term, we must never lose sight of the fact that large, viable populations of ferrets and other endangered species are necessary for the recovery and conservation of these species from an evolutionary standpoint.

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APPENDIX

Calculation of actual adult census number (N) for black-footed ferrets through adjust ment of genetically effective population size (N_e) (Lehmkuhl 1984).

Step 1: Adjustment for variation in progeny number.
$N = (2N_e V_k + 1)/\bar{K}^2$
where N_e = effective population size of 50, V_k = variance in number of young, $\bar{K}$ = mean number of young per female. When lacking data on V_k, multiply 1.4 times N_e.
For the black-footed ferret: $50 \times 1.4 = 70$.

Step 2: Adjustment for unequal sex ratio.
$N_m = (N_e + [\text{male:female ratio} \times N_e])/4$
where N_m = number of males.
$N_f = N_m \times$ female:male ratio
$N = N_m + N_f$
$N/50$ = increase in N_e
N = increase $\times$ 70 (from Step 1)
For the black-footed ferret: (sex ratio data from 1984 census—Forrest et al., in manuscript)
$N_m = (50 + 18/25(50))/4 = 21.5$
$N_f = 21.5 \times 25/18 = 29.9$
$N = 29.9 + 21.5 = 51.4$
$51.4/50 = 1.02$
$1.02 \times 70 = 71.4$

Step 3: Adjustment for overlapping generation.
Double the census number from Step 2.
For the black-footed ferret: $2 \times 71.4 = 142.8$

Step 4: Adjustment for population fluctuations.
Ratio between empirical high and low population cen suses indicates factor with which to increase Step 3 result for MVP estimate.
For black-footed ferret: $43/28 = 1.5 \quad 1.5 \times 142.8 = 214$
$= $ MVP (1983 census $= 28$ adults, $1984 = 43$, Forrest et al., in manuscript)

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SOME GUIDELINES FOR MANAGEMENT OF THE BLACK-FOOTED FERRET

Tim W. Clark

ABSTRACT.—Management guidelines are specified for monitoring and protecting the Meeteetse black-footed ferret (*Mustela nigripes*) population and habitat and for dealing with a series of special management considerations. The Meeteetse ferret population and habitat status are summarized as background. An annual management schedule is outlined, including methods and sources of existing baseline data with which to compare future results. The public support and organizational arrangements needed for successful overall management and recovery of the species are briefly discussed.

This paper outlines some management guidelines for the Meeteetse, Wyoming, black-footed ferret (BFF) population and its habitat. It can serve as a framework for management of other populations, if any can be located or established from Meeteetse BFF stock via captive breeding/translocation. Initially, study plans for the Meeteetse BFFs specifically called for development of management guidelines (Clark 1981, 1984a, b, Black-footed Ferret Recovery Team 1978). These guidelines specify directions for monitoring and protecting the BFF population and its habitat and for meeting certain management considerations. Furthermore, they can focus future discussion by land and wildlife managers as more specific management needs are identified.

BACKGROUND

These management guidelines are based on growing information about BFFs and their chief prey, prairie dogs (*Cynomys* sp.). An annotated BFF bibliography by Casey et al. (1986) lists 351 references, including study results on the Meeteetse BFFs through mid-1985. An earlier summary of BFF biology given by Henderson et al. (1969) and Hillman and Clark (1980) included results of the South Dakota studies (1964–1974). Several prairie dog bibliographies exist: Clark (1971) listed 225 references, Hassien (1973) listed 437, and Clark (in manuscript) lists about 200 citations from 1973 through 1985. History of the Mee-

teetse BFFs and their environment is given by Clark et al. (*Description and history*, 1986), and BFF habitat use patterns are given by Forrest et al. (*Black-footed ferret habitat*, 1985).

MANAGEMENT GUIDELINES

The Meeteetse BFF population was discovered in late September 1981 (Clark and Campbell 1981), and substantial baseline data now exist after 3.5 years of intensive study. Many BFF study methods have been developed and refined and many management needs identified for the population, its habitat, and a series of special considerations.

The Ferret Population

The status of the Meeteetse BFF population is summarized in Table 1. Collectively, field observations from 1981 to 1985 suggest that the BFF population is reproductive, stable, or increasing. It appears to be producing young in excess of number needed to sustain itself. But even an informal risk assessment of the BFF population and its habitat status requires that initial conclusions about the population be evaluated more critically. For example, initial estimates of minimum viable population (MVP) sizes of BFFs, based on conservative genetic estimates, indicate that the Meeteetse BFFs are below numbers recommended for even short-term population viability (estimate that 200 BFF's are needed, whereas 1984 counts showed only 43 adults

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TABLE 1. Status of the Meeteetse black-footed ferret populations (1981–1984).

Parameter	Status			Source
Size (July–August)[1]	1982	1983	1984	Clark 1983, 1984b, 1985a
	61	88	129	
Distribution	BFFs found in a 333 sq km area containing 37 white-tailed prairie dog colonies; total colony area 2,995 ha			Clark et al. *Description and history*, 1986; Forrest et al. *Black-footed ferret habitat*, 1985
Density	Mean 1 adult/56.6 ha; prairie dog colonies over 100 ha contain 2 or more BFFs year-round			Forrest et al. *Black-footed ferret habitat*, 1985
Age and sex structure:	1982	1983	1984	Clark 1983, 1984b; Forrest et al. 1984
Adults/young	21/40	28/60	43/86	
Replacement index	1.90	2.14	2.00[2]	
Female/male:				
Adult	——	——	20/9[3]	
Young	——	——	23/29	
Totals	——	——	43/38	
Natality	1982	1983	1984	Clark 1983, 1985; Forrest et al. 1984; Forrest et al. *Black-footed ferret habitat*, 1985
No. litters	12	18	25	
No. young	40	60	86	
Young/litter	3.33	3.33	3.44	
Mortality	Estimated 55%–75% of total population disappears annually			Forrest et al. *Life history characteristics*, 1985
Imigration/emigration	Unknown, but 15 cases show a mean of 2.5 km			Forrest et al. *Black-footed ferret habitat*, 1985

[1]Minimum counts based on spotlighting surveys (1982 and 1983 counts are believed to be less than actual numbers).
[2]Replacement index = no. young divided by no. adults.
[3]Includes 4 adults (2F and 2M) for 1983.

present; Groves and Clark 1986). Computer simulations of demographic and environmental stochasticity, which may be more important than genetic considerations, are expected to show a MVP different from the 200 estimate. A population target for recovery must be based on a thorough examination of MVP.

This management scheme for the Meeteetse BFF population proposes three monitoring activities: (1) spotlight counts in summer, (2) capture-mark/recapture in fall, and (3) snow tracking and sign searches in winter. The techniques for each monitoring activity, expected data products, and sources of existing baseline data are described in Table 2. Plans of action for protection from (1) harassment, (2) diseases, and (3) predators/competitors are also outlined (Table 2).

The Ferret Habitat

The status of BFF habitat at Meeteetse is summarized in Table 3. Because prairie dog colonies compose BFF habitat (Linder et al. 1972; Clark et al. *Description and history*, 1986; Clark et al. *Descriptive ethology*, 1986; Forrest et al. *Black-footed ferret habitat*, 1985; Houston et al. 1986), BFF habitat management focuses on monitoring and protecting prairie dogs. White-tailed prairie dogs (*C. leucurus*) and the small mammals that

live in their burrows serve as food for BFFs (Campbell et al., unpublished data), and prairie dog tunnels are used for shelter and litter rearing by BFFs. White-tailed prairie dog ethology and ecology have been described by Clark, Hoffman, and Nadler (1971) and Clark (1977). Black-tailed prairie dogs (*C. ludovicianus*) have been described by King (1955), Koford (1958), Hoogland (1981). Gunnison's prairie dogs (*C. gunnisoni*) have been described by Fitzgerald and Lechleitner (1974).

BFF habitat management includes four monitoring activities: (1) recording prairie dog emergence and breeding in late winter, (2) determining prairie dog reproductive success in late spring, (3) mapping active and inactive prairie dog colonies in the region each fall, and (4) surveying alternative prey populations in late summer/early fall. The techniques for each monitoring activity, expected data products, and sources of existing baseline data are described in Table 4. Protection from (1) drastically altered land uses, (2) vegetative alteration, and (3) prairie dog poisoning and shooting are also called for.

Specific Considerations

A host of special considerations surrounding the Meeteetse BFFs require attention, including multiple land use precedents and mandates,

Table 2. An outline of annual monitoring and protec-
tion management needed for the Meeteetse black-footed
ferret population.

I. Monitoring
    A. Use spotlight techniques
        1. Season: Summer, 5 July–30 August
        2. Baseline data sources: Basic spotlight methods
            described by Clark et al. (*Handbook of meth-
            ods*, 1984), Campbell et al. (1985)
        3. Management parameters:
            a. Determine litter numbers, distribution,
                and sizes (results of 1982–1984 litter sur-
                veys given in Table 1 with primary data
                sources)
            b. Check litter behavior and development
                (some behavioral data in Clark et al. [*De-
                scriptive ethology*, 1986])
            c. Determine minimum population numbers
                (results of 1982–1984 estimates in Table 1
                with primary data sources)
    B. Use capture/mark/recapture techniques
        1. Season: Fall, 1 August–15 October
        2. Baseline data sources: Basic capture, handling,
            and marking methods described by Thorne et
            al. (1985), Fagerstone et al. (1985), Forrest et
            al. (1984); results of 1982–1984 surveys shown
            in Table 1 with primary data sources
        3. Management parameters:
            a. Estimate population size
            b. Determine age and sex structure
            c. Determine measurements and body
                weights
            d. Sample ectoparasites
            e. Determine inter- and intracolony dispersal
                and movements
            f. Take other data from captured animals
    C. Use snowtracking and sign searches
        1. Season: Winter, 1 December–1 April
        2. Baseline data sources: Basic snowtracking and
            sign search methods described in Clark et al.
            (*Handbook of methods*, 1984; Clark et al. *Sea-
            sonality of black-footed ferret diggings*, 1984;
            Clark et al. *Descriptive ethology*, 1986), and
            Richardson et al. (1986) results also in these
            sources
        3. Management parameters:
            a. Determine minimum numbers
            b. Determine distribution
            c. Quantify movements
            d. Quantify hunting behavior
            e. Sample intra- and intercolony movements
            f. Estimate onset of breeding
II. Protection
    A. Ascertain levels of human activities
        1. Problem: Harassment
        2. Baseline data sources: Use levels should be
            managed as necessary to approximate pre-1980
            activities, yet allow for needed conservation
            research; general discussions of research im-
            pacts by Clark (1981), Clark et al. (*Handbook
            of methods*, 1984), and Groves and Clark
            (1986); Campbell et al. (1985) described
            spotlight effects on BFFs
        3. Management parameters:
            a. Facilitate site visits by conservation biolo-
                gists, landowners, and others
            b. Limit research impacts
            c. Limit tourists, media, sightseer visits
            d. Monitor traditional land uses
    B. Monitor diseases using standard recognized
        techniques
        1. Problem: Diseases, parasites, disorders
        2. Baseline data sources: Thorne 1984, U.S. Pub-
            lic Health Service, local veterinarians, ranch-
            ers
        3. Management parameters (Thorne 1984):
            a. Sylvatic plague
            b. Canine distemper
            c. Rabies
            d. Pseudotuberculosis
            e. Leptospirosis
            f. Botulism
            g. Stapholococcosis
            h. Tuberculosis
            i. Streptococcosis
            j. Mange
            k. Ear mites
            l. Ring worms
            m. Ticks
            n. Fleas
            o. Human influenza
            p. Others
    C. Use standard monitoring techniques for
        predators and competitors
        (observation, scent stations, live trapping, nesting
        checks, mark/recapture, radiotelemetry, etc.)
        1. Problem: Predators/competitors
            a. Avian—owls, hawks, eagles
            b. Mammalian—long-tailed weasels, skunks,
                badgers, bobcats, coyotes
        2. Baseline data sources: B. Phillips (unpublished
            data) on raptor populations in the BFF area
        3. Management parameters:
            a. Estimate predator/competitor populations
            b. Estimate effects of predators and competi-
                tors on BFFs

oil/gas development, hunting/trapping, live-
stock grazing, road and fence construction,
catastrophes (e.g., diseases), cooperation of
the local public and ranchers, and private/
state/federal interorganizational arrange-
ments needed to monitor and protect BFFs
and their habitat.

Multiple Land Uses.—The Meeteetse
BFFs occupy an area managed under various
state, federal, and private multiple land use
philosophies and mandates. Many traditional
land uses (e. g., livestock grazing) are compat-
ible with BFFs. The extent to which each land
use can enhance or harm BFFs must be exam-
ined from a comprehensive, analytical, "cu-
mulative effects" viewpoint (e.g., see U.S.
Forest Service et al. 1985). A model predict-
ing cumulative effects should be developed,
constantly updated, and used to inform all
management decisions.

TABLE 3. Status of the Meeteetse black-footed ferret habitat (1981–1985).

Parameter	Status			Source
Location	Park Co., western Big Horn Basin, Wyoming			Clark 1985a; Clark et al. *Description and history*, 1986; Forrest et al. *Black-footed ferret habitat*, 1985
Geology/Soils	Dominated by Absaroka volcanics, soils shallow (1 m), well drained and clay-loam, derived from shale parent materials			Clark et al. *Description and history*, 1986
Topography	Broad flat plains at foot of Carter Mountain dissected by creeks, elevation 1890 m			Clark et al. *Description and history*, 1986
Climate	Ranges from 40.5 C to −43.3 C, 173 days each year below 0 C, winds estimated average 13–16 kph, snow usually less than 10 cm accumulation, precipitation averages 30 cm per year			
Vegetation	Junegrass (*Koeleria cristata*) and sagebrush (*Artemisia tridentata*)			Collins and Lichvar 1986
Prairie dog colonies	37 colonies exist in the ferret area, total 2995 ha, mean 80.9 ha ($\pm$ 217.2 ha, range 0.5–1307.0)			Clark et al. *Description and history*, 1986
Prey	Analysis of 86 scats showed 87% prairie dogs			Campbell et al. in ms.; Clark et al. *Descriptive ethology*, 1986; Powell et al. 1985
Ownership:	Private	State	Federal	Clark et al. *Desription and history*, 1986
Surface	35.6%	31.0%	33.4%	
Subsurface	12.0%	31.0%	57.0%	
Potential conflicts	Oil/gas full field development, some development has already occurred			Clark et al. *Description and history*, 1986

A "zone" management plan can facilitate management decisions: (1) Zone I is the BFF-occupied prairie dog complex and a 1.2 km buffer zone, (2) Zone II is the nearby unoccupied prairie dog colonies, and (3) Zone III is the remaining prairie dog colonies in the Big Horn Basin. The BFF zone management plan and cumulative effects analysis could be patterned after the Yellowstone grizzly bear and the northern Rocky Mountain wolf habitat management plans and cumulative analysis models (U.S. Forest Service 1979, U.S. Forest Service et al. 1985, Northern Rocky Mountain Wolf Recovery Team 1985). The Montana Bureau of Land Management (BLM < n.d.> 1982) devised a habitat management plan for the prairie dog ecosystem, and the Wyoming Bureau of Land Management, Cody Resource Area (in preparation) is preparing a similar plan for the Big Horn Basin. These plans can serve as background for a management team to produce more specific and protective plans for the Meeteetse BFFs. Hubbard and Schmitt (1985) listed several recommendations for conserving prairie dogs, including (1) conserve prairie dogs statewide, (2) detour impacts around prairie dog colonies, (3) protect prairie dogs against plague, and (4) apply single use management (i.e., conserve prairie dogs) to key areas.

OIL/GAS EXPLORATION AND EXTRACTION. — The Meeteetse region contains several oil/gas fields (Clark et al. *Description and history*, 1986), and geophysical exploration has been conducted throughout the Meeteetse BFF area on numerous occasions since the early 1950s. Oil/ gas exploration and extraction could have detrimental effects on BFFs by destroying prairie dogs and prairie dog habitat and by directly harming BFFs (U.S. Fish and Wildlife Service 1982). The two common oil/gas exploratory techniques are vibroseis, which uses large truck-mounted vibrating devices to generate shock waves, and explosive charges, which are detonated on or below the surface. These shock waves may affect prairie dogs and BFFs by collapsing tunnel systems, causing auditory impairment, disrupting social systems, or other mechanisms. U.S. Fish and Wildlife Service (1982) proposed study of seismic activities, and such studies are now underway (George Menkens, personal communication).

Extraction of oil/gas may affect BFFs and their habitat detrimentally. Full field development would be most detrimental. Among the potential problems are (1) pad construction and well operation will reduce BFF habitat, (2) leakages and spills could kill BFFs and eliminate habitat, (3) increased vehicle traffic may result in road-

Table 4. A management outline for annual monitoring and protection of the Meeteetse black-footed ferret habitat.

I. Monitoring
  A. Make visual counts of prairie dog numbers and distribution
    1. Season: Spring, 5 May–5 June
    2. Baseline data sources: Clark et al. (*Descriptive ethology*, 1986), Fagerstone (1986)
    3. Management parameters:
      a. Determine total numbers, age structure, aboveground litter sizes, and distributions
      b. Check litter behavior and development (Clark 1977)
      c. Estimate biomass
  B. Remap extent of prairie dog burrow mounds throughout the area, noting areas of active/inactive colonies
    1. Season: Fall, August–September
    2. Baseline data sources: Clark et al. (*Description and history*, 1986), Forrest et al. (*Life history characteristics*, 1985)
    3. Management parameters:
      a. Determine total increase or decrease in prairie dog colonies
      b. Determine the cause of increase or decrease
  C. Note prairie dog emergence times and onset of reproductive activities, quantify prairie dog breeding numbers and distribution
    1. Season: Winter, February–March
    2. Baseline data sources: Clark et al. (unpublished data), Clark (1977)
    3. Management parameters:
      a. Direct observation
      b. Sampling
II. Protection
  A. Land use instability
    1. Season: Annually
    2. Baseline data sources: Clark et al. *Description and history*, 1986
    3. Management parameters:
      a. Map land use patterns
      b. Determine history of land use patterns
  B. Vegetative instability
    1. Season: Annually
    2. Baseline data sources: Collins and Lichvar 1986
    3. Management parameters:
      a. Map plant communities
      b. Monitor dynamics of plant communities
      c. Monitor livestock interactions
  C. Fires
    1. Season: Annually
    2. Baseline data sources: Fire history unknown
    3. Management parameters:
      a. Determine fire history
      b. Develop fire prevention strategy
  D. Prairie dog poisoning and shooting
    1. Season: Annually
    2. Baseline data sources: Clark et al. 1985, Fagerstone 1986
    3. Management parameters:
      a. Determine history
      b. Prohibit or limit poisoning and shooting

killed BFFs, (4) increased human presence may significantly increase the potential for BFF mortality via diseases (e.g., canine-borne diseases) and BFF spatial displacement, and (5) overhead power poles will serve as raptor perching sites, thereby increasing the raptor population and their hunting effectiveness.

Many management options exist to avoid the harmful effects of these oil/gas related actions on BFFs—lease trades and extensions by the federal and state regulatory agencies, directional drilling, burying power lines underground, restricting times of human activities to midday, and other techniques should all be considered as means to eliminate detrimental impacts on the BFFs and their habitat.

Big Game Hunting/Trapping. —Big game hunting (i. e., pronghorn, *Antilocapra americana*) has occurred each fall in the BFF-occupied area for many decades. Historic hunting levels have been compatible with BFFs and have been closely monitored by ranchers. Trapping with steel jaw traps for coyotes (*Canis latrans*), badgers (*Taxidea taxus*), skunks (*Mephitis mephitis*), and mink (*Mustela vison*) is not compatible in BFF-occupied areas.

Livestock Grazing. —Domestic livestock alter range vegetation and affect the myriad plants and animals of the grassland ecosystem "more extensively, rapidly, and profoundly than any other of man's range management activities" (Autenrieth 1983:24). Grazing of the Meeteetse rangelands favors the continued existence of prairie dogs, and therefore BFFs. If rangelands were overstocked by domestic livestock so that prairie dogs were in immediate and direct competition with livestock, the BFF population would be expected to suffer.

Roads/Fences. —Roads and fences can affect BFFs directly and indirectly. Additional roads along with uncontrolled access may increase the probability of BFF road-kills. Fences and high gate posts increase raptor perching sites and may thereby expose BFFs to increased predation. Roads and fence construction should be kept to a minimum. However, in the area of existing oil wells and sludge discharge pits, ferret-proof fences could ensure that BFFs would not fall into a pit full of lethal petroleum waste products.

CATASTROPHES. —Specific plans to meet po- tentially catastrophic events (e.g., sylvatic plague outbreak) should include the worse case option to live capture all the remaining Meeteetse BFFs and either translocate and/or take them into captivity. A network of cooper- ative research institutions, zoos, and other facilities needs to be established and readied to receive BFFs on very short notice. This presupposes that adequate monitoring proce- dures are in place to detect catastrophic events as early in their eruption as possible.

LOCAL PUBLIC AND RANCHERS. —Most BFF conservation actions must be carried out with the consent and cooperation of private landowners. The western Big Horn Basin of Wyoming, the area occupied by the BFFs, consists of many relatively large ranches, many established in the 1870s-1880s. A sensi- tive conservation program must encompass landowner rights and values. Flath and Clark (1984) described an approach that guides the program in Montana to locate and recover BFFs. Frequent contacts in an informal set- ting with ranchers to discuss potential prob- lems has been important in guiding manage- ment directions (Clark 1984a, b). A respect for property rights and a landowner role in the pace and direction of conservation is essential.

ORGANIZATIONAL ARRANGEMENTS. —Sever- al organizational interests are focused on the Meeteetse BFFs—private, national, and in- ternational conservation groups, universities, and an array of state and federal agencies (Clark 1984b). Even though all parties seek BFF conservation and recovery, there are great differences in interest, contributions, plans, and methods to save the BFFs, etc. This fact was noted by Bogan (1985:28.1), who said, "The first [need for the Meeteetse BFFs] is the reconstitution of an advisory board to oversee black-footed ferret research and man- agement. Such a board would include more researchers than at present and would be more inclusive in its consideration of research and management of ferrets." Because the de- sign of coalitions of organizations (e.g., formal organizational arrangements permitting or precluding integration and coordination, joint decision making and goal setting) greatly af- fects the coalition's performance, it is essen- tial that the coalition surrounding the BFF be congruently arranged (i.e., matched) to en-

hance BFF recovery (Nadler and Tushman 1980). The broad design characteristics for such a program and the rationale behind them were given by Clark (1985b). Briefly, program overview should be structured along flexible, "organic" rather than rigid, "mechanistic or bureaucratic" principles (Hrebiniak 1978) be- cause organic organizations are best able to meet the inherent high uncertainty character- istic of the BFF program. Decision-making processes should be open and more formal to avoid the "group think" trap whereby an orga- nization prematurely seeks closure on ideas and discussion of the range of options avail- able to recover and manage a species (Janis 1972). Furthermore, program management must be consistent with the Endangered Spe- cies Act and various state laws.

DISCUSSION

Many more options existed historically to manage BFFs than exist today. Because only a single extant population is known, an en- ergetic proactive management program is needed to ensure their conservation and eventual full recovery. These management guidelines outline actions to monitor and pro- tect the Meeteetse BFF population, its habi- tat, and some special considerations. They are not exhaustive in terms of detail. As other BFF populations are found or established, these guidelines can serve to manage them, too. However, a specific management plan will be needed for each new population. The primary value of general management guide- lines, like these for BFFs, is found in the discussion they may stimulate about the basic requirements and problems needed for suc- cessful species management (Autenrieth 1983). As our understanding of BFFs in- creases, the management guidelines given here may require modification and refine- ment.

Another BFF management requirement not addressed above needs mention. Specific captive breeding/reintroduction plans need to be developed, as called for in 1978 (Black- footed Ferret Recovery Team) and again in 1982 (Clark 1984a), following direction dis- cussed by Richardson et al. (in press), Forrest et al. (*Black-footed ferret habitat*, 1985), and Houston et al. (1986). Potential translocation sites are under evaluation in Montana (J.

Cada, personal communication), Utah (R. Haysanyagaer, personal communication), New Mexico (J. Hubbard, personal communication), and Wyoming (Collins 1985, B. Miller, personal communication). Cooperative planning will allow for a "timely," well organized captive breeding/translocation effort.

There is a risk that the Meeteetse BFFs could become extinct at any time. The extinction risk (as well as the direction and pace of BFF recovery) is difficult to assess because of uncertainties surrounding the BFFs. "Risk" means simply exposure to a danger and is often defined to include the concept of the likelihood (i. e., probability) of damage (Westman 1985). It is strongly recommended that a formal risk assessment be made of both the probability that the Meeteetse BFFs may become extinct and the overall management strategy needed for full species recovery. A meeting involving all the private, state, and federal interests could conduct the needed analysis. Behan and Vaupel (1982) offer procedures to conduct such a risk assessment. These management guidelines, the minimum viable population estimates by Groves and Clark (1986), and the cumulative effects analysis called for are all forms of risk assessment models and could serve, in part, as background for the more formal risk assessment called for here.

Conservation of the Meeteetse BFF population and its habitat as described in this management outline focused almost exclusively on the biological challenge, but it did mention two parallel challenges—sociological and organizational. Essential to conservation of the BFFs is successfully meeting the sociological and organizational challenges simultaneously with the biological challenge.

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BLACK-FOOTED FERRET RECOVERY:
A DISCUSSION OF SOME OPTIONS AND CONSIDERATIONS

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ABSTRACT.—A framework for recovery planning for the black-footed ferret (*Mustela nigripes*) is presented. Current species numbers are probably not sufficient to maintain long-term viability. Three options are presented for increasing ferret numbers: (1) increase available habitat for ferrets where they currently exist, (2) find more wild ferrets elsewhere, and (3) directly manipulate the ferret population through translocation and/or captive rearing. The first two options are either unlikely or currently unfeasible, making it necessary to initiate the third option to ensure ferret recovery. Even if additional ferret populations are located, option three should still be implemented. Three options for direct manipulation to increase ferret numbers and populations are discussed along with accompanying considerations. The captive-rearing/translocation option for species recovery is strongly recommended.

The Black-footed Ferret Recovery Plan (Linder et al. 1978) calls for the establishment of "at least one wild self-sustaining population of black-footed ferrets (*Mustela nigripes*) (BFFs) in each state within its former range." Currently, the species is known from a single population (43 adults in summer 1984, Forrest et al. unpublished manuscript) near Meeteetse, Wyoming. Our initial study efforts focused on evaluating and securing this single population and seeking other populations elsewhere (Clark 1984a). It is now time to address further the long-term goal of BFF recovery.

The purpose of this paper is to provide a framework for recovery planning based on current BFF knowledge largely derived from the Meeteetse studies. We present and dis- cuss options available for increasing species numbers, specifically with regard to the Mee- teetse BFF population, and some consider- ations for choosing among these options.

BACKGROUND AND RECOVERY OPTIONS

Because many states may not have suffi- ciently large prairie dog (*Cynomys* spp.) colonies to support BFF populations, it may no longer be possible or practical to meet the Recovery Plan goal of establishing BFFs in the 12 states within former BFF range. How- ever, BFF recovery will certainly necessitate the establishment of several "self-sustaining"

populations wherever they may be. What size might constitute a "self-sustaining" popula- tion has received much recent discussion. Shaffer (1981) defined a species minimum vi- able population (MVP) as the smallest, iso- lated population having a 99% chance of re- maining extant for 1,000 years despite various natural and biological influences. He pro- posed five methods for determining MVP size: experiments, biogeographic patterns, theoretical models, simulation models, and genetic considerations. Groves and Clark (1986) evaluated the applicability of these methods to endangered species and the BFF in particular. They concluded that two meth- ods are generally unsuitable to estimate BFF MVP size because of lengthy time period re- quirements (experimental methods) that provide little information for current conser- vation needs or because of extensive popula- tion data requirements (simulation models) that might necessitate too long and heavy a research impact on a critically endangered population. They found the genetic method of estimating BFF MVP to be currently most useful.

According to current genetic research, a minimum effective population of 500 or more animals is needed to guarantee the long-term genetic fitness of a species (Franklin 1980, Soulé 1980, Lehmkuhl 1984). Over the short- term (30 generations), a minimum effective population size of 50 should be sufficient to

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prevent an immediate loss of fitness in a population by keeping the increase in inbreeding per generation down to 1% (Frankel and Soulé 1981). Groves and Clark (1986) esti mated that a MVP of 200 BFFs was necessary for maintenance of short-term fitness. They noted, however, that as more data become available, a combination of simulation and ge netic approaches will likely produce the best MVP estimates, because additional important factors, such as environmental and demographic variability, can be incorporated. In deed, Pettus (1985) has suggested that ferrets, as well as other carnivores and some large mammals, may be largely monomorphic, making genetic concerns for maximizing het erozygosity somewhat irrelevant (see Kil patrick et al. 1986). This, and the fact that we have yet to note physical signs of genetic dete rioration or senility in the Meeteetse popula tion, does not guarantee that inbreeding problems will never occur. Carpenter and Hillman (1979) believed that inbreeding con tributed to their lack of success in breeding captive BFF taken from the small South Da kota population in the 1970's.

Whatever method is ultimately used to de termine BFF MVP, one fact remains certain: the single population of approximately 40 BFF adults is inadequate to ensure long-term population fitness and is dangerously vulnera ble to natural catastrophes (e.g., plague or distemper outbreaks) because of its location on one prairie dog complex. Thus, it is imper ative to increase BFF numbers without delay. We have three options for increasing BFF numbers: (1) increase available habitat at Meeteetse, (2) find more wild BFFs at other sites, and (3) directly manipulate BFF num bers, using either direct translocation or cap tive propagation/translocation of the Mee teetse BFFs.

Increasing Available BFF Habitat

Increasing available habitat (and therefore BFF numbers) at Meeteetse is biologically possible. The region contains several large, previously poisoned prairie dog colonies that could potentially be reconstituted by intro ducing prairie dogs. Increasing prairie dog habitat significantly will require several years (estimate 5+) and require additional manage ment. Rancher approval of substantially in creased prairie dog populations on their ranches is problematic. Such an effort would ultimately increase BFF numbers, but the single popula tion would still be highly vulnerable to catastrophic elimination (e.g., plague, distem per). This option seems much less preferable to finding or establishing other BFF populations.

Finding New BFF Populations

Searches for BFFs throughout their former range has been underway in varying degrees for about two decades. Recently improved methods for locating ferrets (Clark et al. *Handbook of methods*, 1984; Clark et al. *Seasonality of black footed ferret, diggings*, 1984) offer a better op portunity to discover additional BFF popula tions if they exist. Because none has yet been found despite new survey methods and in creased survey efforts, we feel it is imperative to institute direct manipulation options to increase BFF numbers and populations. Field surveys should, however, continue to seek other popula tions throughout former BFF range.

Direct Manipulation of BFF Numbers

Direct manipulation options include trans location of some Meeteetse BFFs or captive rearing these BFFs to build up numbers for later release to the wild. Translocation is the direct removal and subsequent release of ani mals from one area to another. Supporting arguments for translocation are: low man power and equipment expenses, use of wild stock, and avoidance of long-term manipula tion, such as captive propagation. Potential disadvantages include: depletion of the source population, need for large numbers of founder animals, high mortality expected among those animals, and lack of a captive reservoir of ani mals from which to control genetic variability, to insure against extinction, and to gather crit ical scientific data.

Past translocation efforts with other species have had mixed success and were typically accompanied by hazards and problems involv ing procedures, suitability of new habitat and release animals, human interest and dedica tion, and funds (Brambell 1977, Perry 1979, Campbell 1980, Temple 1983). Several mustelid species have been translocated, in cluding fisher (*Martes pennanti*, Berg 1982), marten (*M. americana*, Berg 1982, Davis 1983, Frederickson 1983), river otter (*Lutra*

TABLE 1. Notes from past mustelid reintroductions.

Reference	Animal	Period of release	No. animals released	Notes
Benson 1959	fisher	1955–?	6 M, 6 F	population established, Nova Scotia
Weckworth and Wright 1968	fisher	1959–1963	16 M, 20 F	successful, Montana
Williams 1962, 1963	fisher	1959–1963	20 M, 19 F	successful, Idaho
J. Thiebes (Berg, 1982)	fisher	1959–1963	10 M, 14 F	questionable, Oregon
Irvine et al. 1964; Petersen et al., 1977	fisher	1956–1963	78 M, 43 F	successful, Wisconsin, Michigan
C. Douglas (Berg 1982)	fisher	1956–1963	37 M, 60 F	successful, Ontario
Fuller 1975	fisher	1959–1967	19 M, 16 F, 89 unknown	successful, Vermont
Petersen et al. 1977	fisher	1966–1967	30 M, 30 F	successful, Wisconsin (more rapid than above)
Dilworth 1974	fisher	1966–1968	10 M, 15 F	no reproduction, New Brunswick
Pack and Cromer 1981	fisher	1969	6 M, 10 F, 32 unknown	successful, West Virginia
J. Hunt (Berg 1982)	fisher	1972	7 unknown	failed, Maine
R. Leonard (Berg 1982)	fisher	1972–1973	4 unknown	no discernible results, Manitoba
Burris and McKnight 1973	marten	1934–1952	10 M, 16 F, 32 unknown	several populations established, Arkansas
R. Leonard (Berg 1982)	marten	1954	24 unknown	uncertain, Saskatchewan
Jordahl 1954	marten	1953	5 unknown	unknown
C. Douglas (Berg 1982)	marten	1956–1963	155 M, 94 F	successful, Ontario
J. Stuht (Berg 1982)	marten	1957	12 M, 7 F	failed, Michigan
van Zyll de Jong 1969	marten	1960–1969	154 unknown (among 3 areas)	successful in two places, failed in one place, Manitoba
Schupbach 1977	marten	1969–1970	62 M, 37 F	no viable population in 1975–1976, Michigan
Davis 1983	marten	1975–1976	97 M, 27 F	no reproduction recorded by writing, Wisconsin
Frederickson 1983	marten	1977–1983	25 M, 17 F	survival appears high, South Dakota
Jameson et al. 1982	sea otter	1965–1972	708 unknown	three colonies appear successful (Arkansas, British Columbia, Washington), one will likely disappear (Oregon), and one failed (Arkansas)
Goodman, 1981	river otter	by 1981	8 M, 2 F, 45 unknown	success unknown, but sign noted after 18 mos, Colorado

canadensis, Berg 1982), and sea otter (*Enhydra lutris*, Jameson et al. 1982; Table 1). Successful transplants included the use of feasibility studies, solid rather than cage-type traps, the introduction of more than 30 animals (over one or more years), sex ratios favoring females, short handling and transportation periods, and an acclimatization period prior to release. To maximize success, releases were necessary over successive years.

BFF translocations have been poorly documented and offer little evaluation of success. Three BFFs (2M, 1F) were released in Wind Cave National Park in 1953 and 1954 (Garst 1954) after use in the Walt Disney film *Vanishing Prairie*. The last sighting of a BFF there was in 1957. Three BFFs were released on a prairie dog town in Cherry County, Nebraska, in 1957 but were not subsequently reobserved (Badlands National Park records).

Captive propagation takes selected animals into captivity for breeding purposes. Advantages of breeding endangered species in captivity have been discussed by Martin (1975), Carpenter and Derrickson (1981), Frankel and Soulé (1981), and Carpenter (1983) and include: development of a reservoir of animals to insure against extinction in the wild, pro-

TABLE 2. Table of data on black-footed ferrets held in captivity.

No.	Location	Number of animals	Sex	Age at capture	Time in captivity
1	Douglas, Wyoming	1	M	unknown	4 mos
2	New Mexico	1	F	unknown	5 mos
3	New York Zoological Park (NYZP)	1-02700	unknown	unknown	3 mos
4	NYZP	1-02699	M	unknown	1 yr 11 mo
5	NYZP	1-02701	unknown	unknown	3 mos
6	National Zoological Park (NZP)	1 (cat. 11,281)	unknown	unknown	2 yr 2 mo
7	NZP	1 (cat. 7803)	unknown	"young"	unknown
8	NZP	1 (cat. 7804)	unknown	"young"	3 yr 5 mo
9	NZP to London Zoo	1 (cat. 7805)	unknown	"young"	3 yr 8 mo
10	NZP	1 (cat. 7494)	F	unknown	2 yr 7 mo
11	NZP	1 (cat. 7802)	F	unknown	5 yr 1 mo
12	NYZP	1 ——	unknown	unknown	——
13	NYZP	1 ——	M	unknown	——
14	South Dakota	1	M	unknown	1 yr 7 mo
15	South Dakota	2	1 M, 1 F	unknown	unknown (short)
16	Patuxent	4	F	juvenile	"shortly"
17	Patuxent	1	M	juvenile	6 yr[+]
18	Patuxent	1	M	juvenile	4 yr[+]
19	Patuxent	1	F	juvenile	‾6 yr
20	Patuxent	1	M	adult	5 yr[+]
21	Patuxent	1	F	adult	5 yr[+]

duction of stock for release into the wild, col-
lection of life history and behavior data
unattainable in the wild but critical for future
conservation and reintroduction efforts, and
development of public education programs
that will aid in enlisting support for rare ani-
mals. However, captive propagation efforts
must also be seen as one part in the larger

conservation effort, accompanied whenever
possible by parallel programs for conservation
of the natural habitat and the reestablishment
of self-sustaining populations in the wild
(Martin 1975, Durrell 1975, Warland 1975,
Carpenter and Derrickson 1981). Potential
disadvantages include: possible diversion of
funds and interest away from habitat protec-

Year captured	Year died	Cite	Remarks
August 1953	released in Wind Cave National Park December 1953	Garst 1954	Warren Garst, keeper
December 1929	1930 (killed)	Aldous, 1940	Biological Service Collection 1210, caught during prairie dog gassing operations
received 10 April 1928	8 July 1928	NYZP record	Gift of W. J. Brunner
received 18 September 1903	19 August 1905	NYZP record	Gift of Mr. Beebe; remains at America Museum of Natural History (AMNH)
received 10 April 1928	6 July 1928	NYZP record	Gift of W. J. Brunner
received 19 September 1923, Pine Ridge, South Dakota	4 November 1925	NZP record	remains at U.S. National Museum (USNM)
received June 1910, Wallace, Kansas	prior to 30 June 1914—not reported	NZP record	
received 17 June 1910, Wallace, Kansas	26 November 1913	NZP record	no autopsy
received 17 June 1910, transferred 2 February 1911, received 16 February 1911, Wallace, Kansas	25 February 1914	NZP record, London Zoo record	
received 3 April 1909, Wallace, Kansas	2 November 1911	NZP record	USNM—skull; died of congestion of lungs
received 17 June 1910, Wallace, Kansas	2 July 1915	NZP record	remains at USNM
——	June 1888	AMNH record	remains at AMNH 2546-skin
spring 1905	June 1906	AMNH record	remains at AMNH 22894
caught June 1962; received USD 16 February 1963, Reliance, South Dakota	2 February 1964 at USD	Progulske, 1969	held 7 mo at mink ranch, then 1 yr at University of South Dakota
fall 1958, Faith, South Dakota	1 killed, 1 released	Henderson et al. 1969	
fall 1971, Mellette County, South Dakota	1971	Carpenter et al. 1976; Carpenter and Hillman 1979; Carpenter, personal communication	died from vaccination, live distemper virus
fall 1971, Mellette County, South Dakota	11 February 1978	"	died from neoplasia
fall 1971, Mellette County, South Dakota	1 July 1976	"	died from diabetes mellitis and complications
1972, Mellette County, South Dakota	2 October 1978	"	died from neoplasia
1973, Mellette County, South Dakota	9 April 1979	"	died from neoplasia
1973, Mellette County, South Dakota	2 January 1979	"	died from neoplasia

tion, depletion of the source population, and ethical and philosophical arguments against manipulating evolution or maintaining and manipulating wild animals in captivity.

Several mustelids have been successfully raised in captivity, including weasels (*Mustela nivalis*, Hartman 1964; *M. frenata*, Wright 1948), river otter (Johnstone 1978), Siberian polecats (*M. eversmanni*, Carpenter and Hillman 1979; Svendsen, personal communication), European polecats (*M. putorius* and *M. furo*, Buchanen 1966; Williams 1976), mink (*M. vison*, numerous mink ranchers), and marten and fisher (F. Gilbert, personal communication). Carpenter and Hillman (1979) attempted to breed BFFs at the U.S. Fish and

Wildlife Service's Patuxent Wildlife Research Center in the early 1970s and attribute their lack of success to genetically inferior stock. They are optimistic about the success of future captive propagation of BFFs using healthy stock. BFFs have been held in captivity for periods up to several years (Aldous 1940, Progulske 1969, Carpenter and Hillman 1979; Table 2). From this, it is highly likely that Meeteetse BFFs can be successfully maintained and bred in captivity. The following discussion examines direct manipulation options more specifically, applying current BFF knowledge to them.

SOME TRANSLOCATION AND CAPTIVE-REARING OPTIONS AND CONSIDERATIONS

Some of the options to increase BFF numbers and populations are described below and include:
1. Direct translocation of BFF stock.
2. Captive-rearing of BFF in a controlled facility.
3. "Semiwild" field-rearing of BFF in out door enclosures.
4. Combinations of the above.

In addition, planning for each direct manipulation option requires addressing five major considerations:
1. Selection of animals for removal from Meeteetse to prevent drastic decline:
   A. Number of animals to be removed.
   B. Animal age and sex.
   C. Time of year animals are captured.
   D. Measures to be taken to ensure genetic variation among animals.
2. Assessment of rearing and release sites:
   A. Size and location of site.
   B. Status of prey base at translocation or field-rearing sites.
   C. Disease and parasite vectors at new sites.
   D. Predator management/control.
   E. Release site security.
   F. Time and resources needed to assess sites.
3. Captive facilities, animal care and costs:
   A. Facility specifications, expertise, per sonnel, equipment, and costs.
   B. Enclosures for animals and costs.
   C. Dietary requirements for animals and costs.

D. Procedures to breed animals.
E. Procedures for care of new litters.
F. Commitment needed for facility.
G. Public education.
H. Time needed to establish facility.
4. Release considerations:
   A. Methods—immediate or gradual.
   B. Minumum numbers—age and sex.
   C. Procedures to prepare captive animals physiologically and behaviorally for re lease into the wild.
   D. Monitoring released animals—marking methods.
   E. Long-term management needs for habitat and for maintaining genetic variation.
   F. Local support and education.
   G. Time needed to develop release stock.
5. Biological data:
   A. Essential information needed for BFF recovery.
   B. Biological data gained from any of the direct manipulation options.

Selection of Animals for Removal from Meeteetse

The major consideration in removal of BFFs from the Meeteetse population is maintaining a sufficient number of animals there to ensure continuation of that population. To do this, we must generally minimize removal of existing breeding stock (i.e., adults) and select adults and juveniles at a number less than that re quired for recruitment to maintain the cur rent population.

NUMBER OF ANIMALS TO BE REMOVED.—The number of BFFs removed from Meeteetse in any one year should be derived from ongoing research (litter counts, litter sizes, litter dis tribution, population estimates, age and sex data, mortality rates, etc.). A successful translocation must release enough animals each year to surpass animal losses to preda tion, dispersal, injury, etc. Berg's (1982) re view of mustelid reintroductions emphasized that a minimum of 30 animals should be re leased to an area over a minimum of four consecutive years to ensure establishment of a new population. Temple (1983) suggested it may take even longer. We describe a hypo thetical direct translocation scenario for re moval of BFFs from Meeteetse below (Fig. 1).
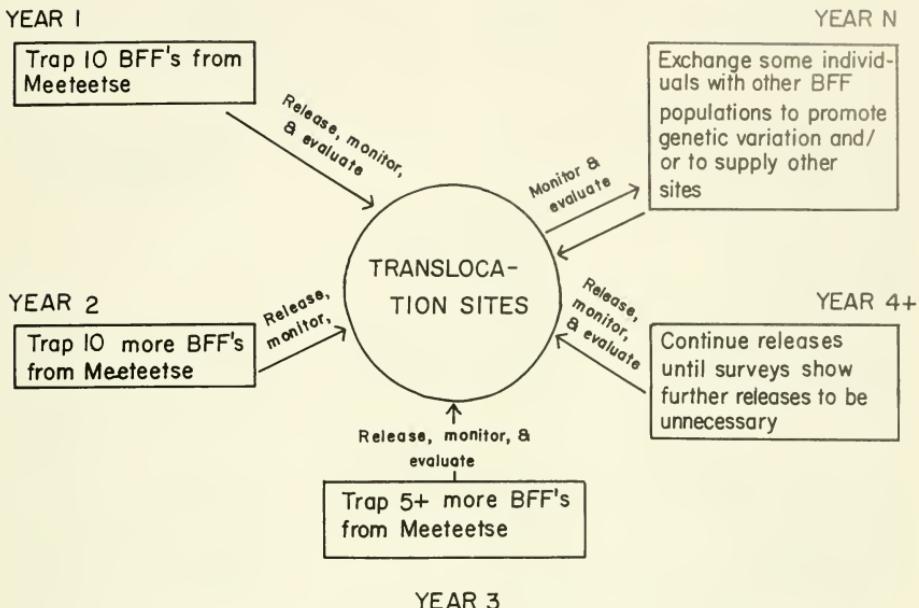
Fig. 1. Hypothetical direct translocation scenario for removal of black-footed ferrets from Meeteetse.

By contrast, fewer animals should be re-quired overall to establish a captive BFF pop-ulation, assuming breeding of ferrets is suc-cessful. Recommended numbers of founder individuals for establishment of captive popu-lations range from five (Senner 1980) to 10 (Chesser et al. 1980) to 5–10 pairs (Foose and Foose 1982). Thus, it may be possible in a few years to have captive-reared surplus animals for release to one or more areas, requiring extremely low removal rates from the Mee-teetse population. This may prove important if the population declines or if it is suspected that high numbers of juveniles are needed to counterbalance mortality factors and thereby ensure adequate population recruitment. A hypothetical captive-rearing scenario is pre-sented below (Fig. 2).

AGE AND SEX.—Juvenile BFFs should prob-ably be used in the direct translocation op-tion, because this option involves potentially high post-transfer mortality and because inex-perienced juveniles may be more "expend-able" than experienced breeding adults. Con-versely, we suggest that the first animals taken into a captive propagation program in-

clude at least two to three proven breeders, con-tingent upon maintenance of a satisfactory wild Meeteetse population size. Sex ratios should fa-vor females for removal, possibly 2 or 3:1. We project a 2–3 year period is needed in a captive-rearing effort to perfect breeding techniques. Having only inexperienced breeders in hand may only compound difficulties in development of needed techniques, as well as delay produc-tion of captive and release stock. The mortality risk to captive individuals is assumed small, and, although separated from the wild population, they could be returned to it at any time if neces-sary.

TIME OF CAPTURE.—Juvenile BFFs should be trapped after weaning but while it is still possible to distinguish them from adults (late August to mid-September). There may also be advantages early in a captive-rearing program to trapping adult females after breeding in May to increase the probability of their bearing litters the first year in captivity. This would have to be weighed against the potential risk of trauma to these fe-males.

MEASURES TO ENSURE GENETIC VARIATION.—With a direct translocation option, genetic varia-
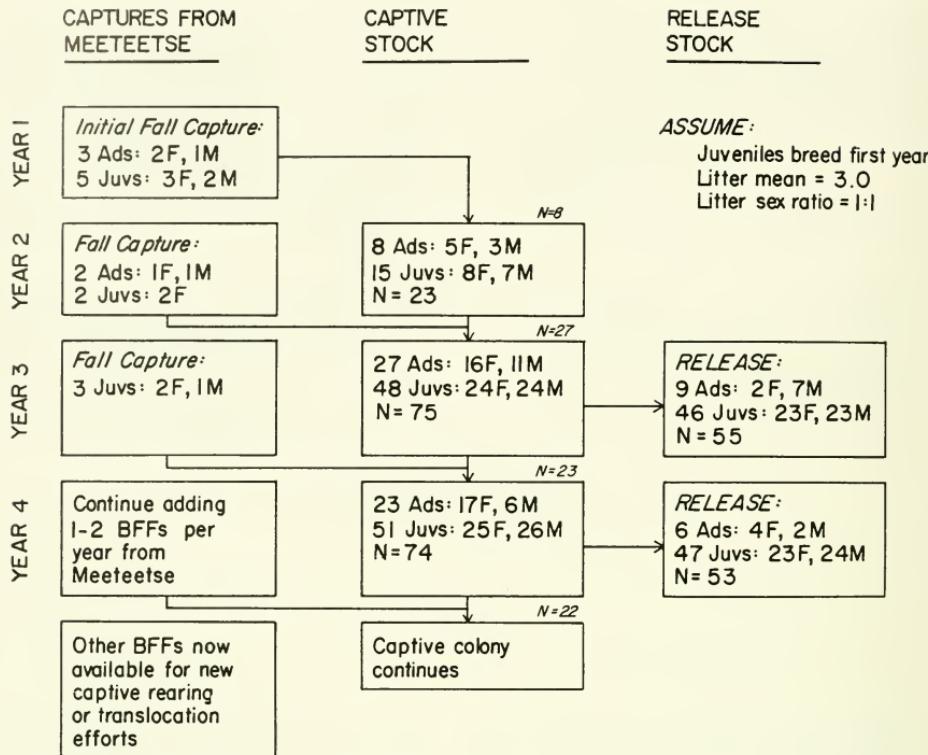
Fig. 2. A hypothetical captive-rearing scenario for black-footed ferrets.

tion could be ensured only by capturing BFFs from different parts of the Meeteetse complex to minimize relatedness. Selective breeding cannot be accomplished. However, future re leases could introduce new genetic material to the release population.

By contrast, a captive propagation program permits selective breeding to maximize ge netic variation and avoid inbreeding prob lems. Although it may eventually be decided that maintenance of heterozygosity is not as critical as environmental and demographic factors in maintaining population fitness, we should initially plan a strategy of genetic man agement. Foose and Foose (1982) describe a four-step general strategy for the genetic management of captive populations: (1) Ac quire an adequate number of founders as un related and non-inbred as possible (from Mee teetse, this would mean from various parts of the complex); 5 to 10 pairs of unrelated and

non-inbred founders would contain over 90% of the average diversity of a given gene pool. (2) Expand the population as fast as possible to facility(ies) carrying capacity to maximize the genetic contribution of each founder. This means that the short-term minimum effective population of 50 can be derived from a small number of founders as long as each one is well-represented in the expanding popula tion. (3) Possibly subdivide populations be tween two or more facilities, closely regulat ing the exchange of genetic material among them. (4) Within any subdivisions, (a) maxi mize minimum effective population by maxi mizing number of animals that actually re produce, (b) equalize founder representation, and (c) manage inbreeding coefficients. Frank lin (1980) recommends the inbreeding coeffi cient be no more than 1% per generation.

Such a strategy should be adopted for breed ing BFFs in both the captive-rearing or field-

rearing options. This will help mitigate the double genetic bottleneck described by Temple (1983), which is caused by first choosing a small number of animals to be taken into captivity and second by taking only a selection of their offspring to be released. Studbooks should be maintained to record breeding histories (Mohr 1968).

Assessment of Rearing and Release Sites

SIZE AND LOCATION OF SITE.—Direct translocations or field-rearing with subsequent releases using BFFs from Meeteetse should first be considered on white-tailed prairie dog colonies (*Cynomys leucurus*). Behavioral differences of black-tailed (*C. ludovicianus*) and Gunnisons (*C. gunnisoni*) prairie dogs might potentially affect the success of BFFs raised on white-tailed colonies and translocated to colonies of other species. It is unknown whether captive-reared BFFs can equally adapt to the three prairie dog species. Eventually BFFs should be released to colonies of all three prairie dog species.

We suggest 40–60 ha/BFF be used to calculate size of translocation sites (Forrest et al. 1985). Black-tailed prairie dog colonies may possibly support a BFF on smaller areas because of their higher population densities, but currently we have no evidence for this. Ideally, any release site would be capable of supporting a minimum of 50 adult BFFs to allow for an initial rapid expansion of the population to minimize the loss of genetic variability (Chesser et al. 1980, Foose 1983) and to reduce the need and costs for genetic management (i.e., breaking up inbreeding groups and introducing new animals in future years). This would be 2500–3000 ha of active prairie dogs with a burrow density of $10+$/ha (Forrest et al. 1985). However, smaller areas could be used in the overall recovery scheme if animals were occasionally mixed between populations. To achieve recovery, areas or combinations of areas supporting more than 500 BFFs will be required. Forrest et al. (1985) and Houston et al. (1986) discuss further details of BFF translocation site requirements.

Size considerations for a captive-rearing or field-rearing facility should be determined by space requirements per animal and the number of animals the facility should expect to hold (discussed below). Location of any such facility should seek to approximate or control for the environment of Meeteetse and have ready access to any necessary additional facilities or expertise not directly part of the captive-rearing facility (e.g., additional veterinarian, scientific, or technical staff, laboratory facilities, etc.). A field-rearing facility would be located on or adjacent to a release site, which may not have ready access to other facilities.

PREY BASE STATUS.—At least one season prior to any release or establishment of a field-rearing facility, status of the wild prey base should be assessed to ensure that it is healthy and viable. We suggest that monitoring of the prey base continue after releases as well.

DISEASE AND PARASITE VECTORS.—Prey should be screened for disease or parasite vectors, and plague potential should be assessed through local inquiry and examination of potential carriers. These precautions should also be taken on sites where fresh prey might be obtained to supply a captive-rearing facility.

PREDATOR CONTROL.—Short-term predator management should be considered at release sites. Removal of nearby raptor nests or perches and trapping and removal of badgers (*Taxidea taxus*), coyotes (*Canis latrans*), bobcats (*Felis rufus*), skunks (*Mephitis mephitis*), and foxes (*Vulpes* sp.) in the immediate area should be attempted. Predators, as well as excessive human disturbance, should be controlled at any facility housing captive animals.

RELEASE SITE SECURITY.—A major factor to consider when assessing release sites is obtaining long-term guarantees against prairie dog poisoning and extensive habitat alteration from landowners and/or agencies prior to the release. Grazing and some recreational land uses are acceptable.

TIME AND RESOURCES NEEDED TO ASSESS SITES.—Assessment of rearing sites for BFFs can probably be easily accomplished at relatively low cost and over one season. Initial assessment of release sites may take a couple of seasons, and obtaining necessary management agreements and protection guarantees could conceivably take longer. Cost and time of periodic site monitoring after releases must also be considered. It is critical that planning for translocation sites be done in conjunction with planning for captive-rearing facilities to

make sure that release sites are available when suitable BFF stock has been reared.

Facilities, Animal Care, and Costs

Facilities.—Direct translocation will not require construction of a facility and is therefore the lowest cost option. Only holding boxes or cages will be needed during trapping, transportation, and release. Conversely, the captive-rearing option is certainly the most costly, and either requires building new or remodeling existing facilities with at least one permanent staff person. Any facility should include: (a) a food preparation and storage area, (b) an isolated quarantine area, (c) an emergency nursery, (d) various enclosures, (e) waste disposal and proper drainage, (f) water and electricity, (g) possibly a viewing area for the public, (h) a well-constructed boundary fence, (i) storage space for tools or equipment, (j) ready access to laboratory and veterinary facilities, (k) quarters for staff person(s). Frankel and Soulé (1981) remark that a consultant behaviorist familiar with the species (and closely related species) is mandatory to advise on which individuals should form the founding nucleus of the captive population and what enclosure "furniture" and structures will produce proper development and behavior, including proper hunting and escape behaviors after release.

For the field-rearing option, we envision a lower maintenance portable facility to be used over many years at successive sites, which would also require permanent staff. Costs would include site assessment, construction of a series of large, totally enclosed pens, staff salary, and veterinary and laboratory costs. A quarantine area, a storage area, and some access to veterinary and laboratory facilities would be needed. Many of the same costs are required as with a captive-rearing facility. The main difference here is that the facility is portable and has a lifetime dependent on the number of release animals needed for a particular site.

Enclosures.—Like other mustelids, BFFs are typically solitary animals and should be kept in individual enclosures, except during breeding or when raising young. Enclosures for transporting animals and making direct translocations may be small plywood holding boxes with adequate ventilation and bedding. A proper lining is needed to prevent excessive BFF toothwear and breakage.

Management procedures have been described for BFFs kept at Patuxent Wildlife Research Center (Carpenter 1977, Carpenter and Hillman 1979, Hillman and Carpenter 1983). BFFs were housed in individual pens consisting of: (1) a two-compartment nest box that could be illuminated to permit observation through a one-way glass mirror, (2) a one-inch mesh welded wire intermediate area where food and water were provided and where defecation and urination generally occurred, (3) a wooden runway exercise area with an exercise wheel, and (4) a darkened artificial burrow below the exercise area. Facilities and equipment were routinely cleaned and disinfected. BFFs were housed alone in a well-ventilated pole barn-type building, fully daylighted and with clear plastic screened panels to protect against wind and cold temperatures.

Additional suggestions derived from observation of Jersey Wildlife Preservation Trust (Channel Islands, U.K.) procedures include a second nest burrow for choice and a variety of "furniture" in the enclosure providing various hiding places, variation in environment, and playthings. It is essential that BFFs have areas into which they can retreat and be assured that they are secure from any invaders or stressful conditions.

We have suggested a breeding stock of about 20 animals, ultimately providing about 50 release animals per year (Fig. 2). If one facility is used, it may have to house up to 70 BFFs at peak periods. We suggest dividing breeding stock among a few facilities to make better use of expertise at those facilities, to prevent catastrophic loss from disease outbreaks, and to reduce inadvertent selection from the rearing environment at any one facility. Several European ferrets (*Mustela putorius*) or Siberian ferrets (*M. eversmanni*) should be acquired to serve for experiments or as surrogate mothers.

For the field-rearing option, large pens would be used constructed of wire mesh, including a top, perhaps in a long rectangular shape, with a wire mesh bottom covered with about a 1 m soil layer. "Furniture" would be needed and perhaps a series of artificial burrows. Pens should be constructed to allow

mixing of certain animals. Observation blinds and possibly an external light source should be considered to allow use of a starlight scope. Extra pens may be necessary to allow rotational use and cleaning. Size of the facility would be geared to the number of animals planned for release to that area.

DIET.—Animals at direct translocation sites may require a short period of feeding, including live prey from the new area. Ideally, food for captive animals should be as fresh and as natural as possible, especially considering that some animals will be returned or released to the wild. Live prey is certainly important for developing proper predatory behavior in young and can be used as a supplement for breeders and for variation from commercial diets. Progulske (1969) fed a BFF ground food consisting of jackrabbits, liver, meat scraps, fish, and dietary supplements. The animal did not eat dead small mammals even when the ground food was removed. Live prairie dogs were released on several occasions, which the BFF killed and fed upon. Carpenter and Hillman (1979) fed BFFs canned feline diet. Breeding diet was supplemented with fresh liver and small quail, and lactating females were provided with an artificial feline milk substitute. We presented dead prairie dogs to BFFs, as did Hillman (1968); they were quickly dragged down burrows. We have noted BFFs taking cottontail rabbits (*Sylvilagus nuttallii*), ground squirrels (*Spermophilus elegans*), and mice (*Peromyscus maniculatus*) as prey (Richardson et al., unpublished data).

Besides commercial diets, we suggest raising small mammals (rabbits, prairie dogs, mice, guinea pigs, etc.) adjacent to the facility (to minimize problems with parasites in the food) to supplement diets and for behavioral learning. At Jersey Wildlife Preservation Trust, whole carcasses are considered important in carnivore diets to provide psychological benefit to the animal (a carcass providing a variety of textures and gnawing surfaces) as well as nutritional benefit, even though costs for providing whole carcasses are higher than for commercial diets. Care should be taken in releasing live prairie dogs with BFFs, because we believe the prairie dogs are capable of inflicting serious injuries to some BFFs. Vitamin/carnivore supplements would be recommended.

PROCEDURES FOR BREEDING.—Breeding could not be controlled in the direct translocation option, but it would be in a captive-rearing option. Procedures for breeding BFFs in captivity have been discussed by Carpenter and Hillman (1979) and Hillman and Carpenter (1983). Females in estrus can be recognized by vulvar swelling and confirmed by vaginal smears. Carpenter and Hillman (1979) placed a male in with estrus females for two to three successive nights during the peak estrus period, removing him post-coitus. Observation blinds and starlight scopes were used to monitor and record behavior. At the Jersey Wildlfe Preservation Trust, individuals of normally solitary species are often allowed to mix during the breeding period through an opening between their enclosures (Nick Lindsay, personal communication). It is, however, critical that both animals have enough space to avoid interaction if they so desire, which in turn avoids aggressive confrontation. Initial mixings, at least, should be monitored, and the male would be closed out after the female has completed estrus.

Perhaps breeding procedures for the field-rearing option could consist of allowing the mixing of certain animals during breeding season, but in a large enough area to allow retreat to distinct living areas if the animals choose. We have observed male, female, and juvenile BFFs in close proximity (within 100 m of each other) for short periods of time. Intersexual mixing may not be a problem given an adequate opportunity for BFFs to retire from each other.

PROCEDURES FOR NEW LITTERS.—Carpenter and Hillman (1979) were concerned about preweaning losses from females failing to lactate or permit suckling, from mortality caused by the female, and from dietary or environmental factors. They planned to remove litters from their mothers after six weeks. They also observed that a European ferret readily accepted a BFF kit whose mother failed to lactate. It will have to be decided in both rearing options whether greater benefit will come from allowing litters more time with their mothers to approximate the wild condition or from minimizing preweaning losses by removing litters from females after a few weeks.

COMMITMENT NEEDED FOR FACILITY.—It is critical to ensure adequate commitment prior to initiation of any of the direct manipulation options, but especially for a captive-rearing facility, which would require the largest investment of

time and funds. Various avenues for funding should be explored, one successful model being the Peregrine Fund. This is a nonprofit organization that provides funds for peregrine research and recovery efforts from private, state, and federal contributions.

Public education.—A captive-rearing or field-rearing facility should strongly consider offering low-key public education programs to increase project support. This would be especially important in the field-rearing option, where animals would later be released to a nearby site. Programs should, of course, be tailored around the needs of the animals.

Time needed to establish facility.—Facilities for direct translocation, requiring only cages or holding boxes, could be prepared in a matter of weeks. A captive-rearing facility may take from several months to a year to prepare. A portable field-rearing facility would require several months to acquire or construct its various components but should take a relatively short time to assemble once a site were chosen.

Release Considerations

Methods.—Two release methods are generally used: "quick" and "slow." A "quick release" is the immediate release of an animal, with no time spent in a holding facility at the release site. A "slow release" means a gradual acclimatization to the new area, with the animal retained in a holding container or enclosure for a period of time, after which an entry is opened allowing the animal to leave at will. Supplementary feeding is typically done until the animal no longer frequents the release area. Berg (1982) has reviewed a variety of mustelid reintroductions and noted that the slow release method, holding animals up to five days, has been more successful.

Numbers.—We previously discussed BFF numbers to be released in a direct translocation. Ten BFFs would be an absolute minimum number (as in direct translocation) for an initial release, preferably 20 or more. Five or more animals would be added over a minimum of three years, unless subsequent releases are shown to be disruptive to established animals. A preferred sex ratio would favor females at about 2:1. Animals to be released should be old enough and experienced enough to be able to hunt successfully.

Procedures for captive-reared animals.—If animals are directly translocated from Meeteetse, they will need little preparation for release other than a short acclimatization period. A health check (e.g., fecal screen) would be recommended prior to all releases.

With a captive-rearing or field-rearing option, some behavioral adjustment or training (e.g., to hunt and kill prairie dogs, to be wary of predators) may be needed to prepare stock for release. We presently do not know the degree to which young BFFs learn to hunt from their mothers and/or hunt instinctively. We have seen juvenile animals moving about with their mothers as if being taken on an exploratory or hunting foray. In any case, young BFFs should be proven hunters before being released to the wild. A procedure for this will likely have to be developed once the ferrets are in captivity, or possibly with a surrogate species.

Monitoring.—All released animals should be permanently marked, and some or all of the animals in the initial release and some animals in subsequent releases should carry radio-transmitters and be monitored regularly to best understand the fate of released animals and tailor subsequent releases for maximum success.

Long-term management.—A long-term management plan should be established not only to maintain the habitat quality of the area (as mentioned earlier), but also to assure the maintenance of genetic variation between different areas. Such a plan should be specified in advance of any release.

Local support.—In any area where BFFs will be newly released, an effort should be made to gain local public support of the project and to educate people about BFFs, their habits, and those activities that will directly or indirectly harm BFFs. This must be done in a low key manner within the sociological context of the release site (Clark 1984b).

Time needed to develop stock.—The direct translocation option releases BFFs to the wild most quickly, with possibly two seasons needed to establish a site and capture the initial release stock. Time required to develop release animals from a captive- or field-reared stock will likely take a minimum of several years from initial capture, assuming about 10 BFFs are taken into captivity. As in direct

translocation, releases of field-reared stock into one area should occur over a number of years.

Biological Data

What we will learn from translocating ani- mals directly from Meeteetse, assuming at least some animals are marked, is the fate of some BFFs, some BFF movements at the new site, and possibly the breeding history of some females. It must be decided whether or not this is the minimum we need to know about BFFs in such a recovery effort.

Undoubtedly a much larger volume of bio- logical data on BFFs could be gathered if some animals were held in captivity, specifi- cally data on reproduction, parturition, feed- ing and nutrition, juvenile ontogeny and be- havior, maternal care and behavior, defe- cation, activity patterns, genetics, prey acqui- sition and food habits, intraspecific behavior, intersexual behavior, age of sexual maturity, life-span, duration of sexual maturity, age at and behavior during weaning, sibling interac- tions, health, and disease. Most of this is cur- rently poorly understood. Variation in cage design could allow for some observation of underground behavior, since as much as 80% of a BFF's activity occurs there. Techniques for artificial insemination of European ferrets and potentially for BFFs have been devel- oped (Carpenter 1977) and may be considered here.

Less biological data on BFFs would be ob- tained with the field-rearing option because less control and handling of animals would occur. Observations of underground behavior would probably not be possible.

CONCLUSION

Assuming several, large new BFF popula- tions are not found in the immediate future, the plan that best addresses the needs for BFF recovery must use a direct manipulation op- tion (direct translocation or captive propaga- tion/translocation). Certainly translocation should occur either directly or from a captive facility, because suitable BFF habitat still ex- ists in many areas throughout the species' for- mer range. We suspect that a direct transloca- tion of BFFs from Meeteetse is unfeasible because of the direct risk both to the trans- ferred animals and to the Meeteetse popula- tion itself if a large number of animals are removed. Captive-rearing of BFFs is proba- bly the best recovery option because it would guarantee a protected reservoir of BFFs with a controlled lineage, because it would provide the greatest numbers of ferrets for eventual release over the long run, and because of the large amounts of information to be gained by close observation of the animals.

The field-rearing option may not allow close enough monitoring of BFF health and behav- ior or provide access to adequate support facil- ities and expertise, which the responsibility of taking an endangered mammal into captivity dictates. Such an option might be suitable for less rare animals or for BFFs once critical behavioral information and acceptable popu- lation size have been attained. The use of large portable outdoor enclosures may be suitable for some animals at captive-rearing or release sites.

Based on the above discussion, we recom- mend:

1. The first BFFs removed from Meeteetse be housed in a fully equipped captive-rearing facility.

2. A minimum of 10 BFFs be taken from the Meeteetse population over three to four years to establish the above facility, assuming population status there continues at previous levels; a small number of these should be breeding adults to expedite success of breed- ing efforts.

3. The goal of such a captive facility be to raise BFFs for future translocation to the wild; therefore, facilities and expertise should re- flect the behavioral development of "wild- ready" BFF stock.

4. The breeding of BFFs in captivity and subsequent releases of BFFs to new sites be conducted in a way to maximize survival of these individuals as well as genetic diversity.

5. BFFs eventually be housed at more than one facility (perhaps three plus) to make bet- ter use of existing facilities and expertise, to insure against any catastrophic disease out- breaks at one facility, and to reduce any inad- vertent selection due to the rearing environ- ment at any one facility.

6. Translocation sites for BFF be large enough to support a viable short-term BFF population (currently estimated at about 50

adult BFFs) and be part of a managed network of sites that support a viable long-term BFF population (more than 500 adults).

7. A long-term time and resource commitment be made before BFFs are taken into captivity to ensure achievement of BFF recovery; a nonprofit organization, such as the Peregrine Fund Inc., is a suggested model for this.

8. A comprehensive management plan be developed prior to removal of BFFs from Meeteetse addressing facility development, timely designation of release sites, long-term monitoring of release sites, and long-term management of released BFFs. We suggest that strategic management follow the procedure outlined and discussed by Byars (1984). Strategic management includes both planning and implementation concerns. Byars (1984) presents an eight-stage process, including: (1) defining the mission, (2) formulating appropriate policies, (3) establishing long- and short-range objectives, (4) identifying strategic alternatives, (5) selecting the appropriate strategy, (6) developing an organizational structure, (7) managing organizational activities, and (8) monitoring the effectiveness of the strategy and organizational arrangements in achieving the objectives. Because these concerns are interrelated, considerable feedback must occur throughout the strategic management process.

Appropriate decision-making procedures are central to strategic management, and, in the uncertain task environment presented by ferret recovery, formal risk assessments must be a key feature (Behan and Vaupel 1982). Several time-related analytical and graphical techniques have been developed that can be useful in the strategic management planning process, including decision theory and critical path analysis (CPA) and program evaluation and review techniques (PERT). All these techniques use graphical networks to depict various segments of work that must be accomplished to complete a task such as ferret recovery. PERT methods may be more useful for ferret recovery strategic management because the activity durations are somewhat uncertain and variable (Behan and Vaupel 1982).

The future of this unique species is brighter today than in the last few decades. BFF recovery will require a cooperative private, state, and federal program and a closely managed coalition of interests.

ACKNOWLEDGMENTS

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PROGULSKE, D. R. 1969. Observations of a penned, wild-captured black-footed ferret. J. Mammal. 50:147–156.

SCHUPBACH, T. A. 1977. History, status and management of the pine marten in the upper peninsula of Michigan. Unpublished thesis, Michigan Technological University, Houghton. 79 pp.

SENNER, J. W. 1980. Inbreeding depression and the survival of zoo populations. Pages 209–224 in M. Soulé and B. Wilcox, eds., Conservation biology: an evolutionary-ecological perspective, Sinauer Associates, Sunderland, Massachusetts.

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ANNOTATED BIBLIOGRAPHY OF THE BLACK-FOOTED FERRET

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ABSTRACT.—An annotated bibliography of 351 references on the black-footed ferret (*Mustela nigripes*) shows 19 articles, mostly species descriptions, published from 1851 through 1899; 69 papers, mostly describing the range of the species, from 1900 through 1964; 156 papers dealing largely with the Mellette County, South Dakota, ferret research published from 1965 through 1980; and 107 publications since 1981 dealing primarily with the Meeteetse, Wyoming, ferrets.

This bibliography represents the first relatively complete annotated listing of the primary literature on the black-footed ferret. It builds on previous species summaries by Snow (1972), Harvey (1972), and Hillman and Clark (1980). This literature assemblage can serve as a statement of current information on the species and as background for future ferret conservation and recovery efforts.

METHODS

We attempted to limit the references to those containing original data or new information in published books or scientific journals. A few secondary sources and popular articles provide good overviews and were included. No newspaper articles are cited. We used the existing literature in our libraries as well as the Yale University libraries. The literature cited in each article or book was sought for additional references. We feel that the historical literature, prior to 1960, is well represented. The scientific literature on the 1964–1974 South Dakota ferret research is also well covered, but less widely available popular works from these studies are not as well represented. We included some contract consulting reports to governmental agencies that contain valuable information, but some of these were also not readily available. We annotated all publications we saw.

BLACK-FOOTED FERRET LITERATURE

This bibliography contains 351 references, nearly all of which are annotated. Nineteen (5%) were published between 1851 (when the species was first described) and 1899. These articles include the first descriptions of the animal and its range, a decades-long controversy over the existence of the species, calls for more information, and confirmation of the validity and range of the species late in the century. Between 1900 and 1964, 69 (20%) articles were found. These articles focus largely on the distribution of the species along with a few accounts of its ecology and status and the first known photographs of both wild (1929) and captive (1906) animals. Between 1965 and 1980, 156 articles appeared. These largely comprise the Mellette County, South Dakota, studies from 1964 through 1974. These constitute a solid body of scientific data on the life history of wild ferrets, captive rearing attempts, and the status of the species as well as surveys for ferrets. Most of the 107 (30%) publications from 1981 to 1985 deal with the Meeteetse, Wyoming, ferrets—discovered in late 1981, as well as renewed interest in finding or transplanting ferrets in other states. Less than one publication appeared every two and one-half years for the first 50 years of our knowledge of ferrets. About one paper was published per year from 1900 through 1964. This rate jumped to 10 papers per year from 1965 to 1980 and then to 27 per year after 1981.

We realize that new publications will be forthcoming. We welcome additions to this bibliography, and we apologize for any citations that were inadvertently overlooked.

[1]Biota Research and Consulting, Inc., Box 2705, Jackson, Wyoming 83001.
[2]Yale University, School of Forestry and Environmental Studies, New Haven, Connecticut 06511. Present address: Ecology and Environment, Inc., 195 Sugg Road, Post Office Box D, Buffalo, New York 14225.
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BAILEY, V. 1905. Biological survey of Texas. U.S. Biol. Surv. North Amer. Fauna No. 25. U.S. GPO, Washington, D.C. 226 pp.

Notes several occurrences of BFFs in Texas and cites Cary (1902) for reports from Stanton, Texas.

———. 1926. A biological survey of North Dakota. U.S. Biol. Surv. North Amer. Fauna No. 49. U.S. GPO, Washington, D.C. 226 pp.

Early scientific description of North Dakota mammals, including *Mustela nigripes*.

———. 1932. Mammals of New Mexico. U.S. Biol. Surv. North Amer. Fauna No. 53. U.S. GPO, Washington, D.C. 412 pp.

Very brief account concluding with the thought that "high living on easily obtained fat prairie dogs seems to be the only explanation of their scarcity."

BAILEY, V., W. P. BELL, AND M. A. BRANNON. 1914. Preliminary report on the mammals of North Dakota. North Dakota Agric. Expt. Sta. Circ. No. 3, Fargo. 20 pp.

BAIRD, S. F. 1857. General report on the mammals of North America, the descriptions of species based chiefly on the collections in the museum of the Smithsonian Institution. Philadelphia, J. B. Lippincott & Co. 764 pp.

Brief description of BFF based entirely on Audubon and Bachman's description. Notes that "it is a little remarkable that so conspicuous and well marked a species should have eluded the notice of the recent explorers in the Platte region."

BAKER, A. B. 1889. Mammals of western Kansas. Trans. Kansas Acad. Sci. 11:56–58.

Describes BFF as predator of prairie dogs and as "nowhere numerous."

BANFIELD, A. W. F. 1974. The mammals of Canada. University of Toronto Press. 396 pp.

BELITSKY, D. 1985. Black-footed ferret habitat management in Meeteetse. Pages 5.1–5.4 *in* S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.

Currently managed for livestock grazing and big game range, BFF habitat near Meeteetse is protected from major impact by suspension of proposed oil field development until other management strategies can be implemented.

BERYMAN, J. H., AND N. C. JOHNSON. 1973. Ferret and prairie dog programs on public lands: a perspective and some facts. Pages 109–125 *in* R. L. Linder and C. N. Hillman, eds., Proc. Black-footed Ferret and Prairie Dog Workshop, South Dakota State University, Brookings.

Bureau of Sport Fisheries and Wildlife lobbied for rational management of prairie dog colonies. Points out the USDI policy conflict of energy production vs. resource protection. Emphasizes need for compromise policies. Includes 1965 USDI BFF policy statement and 1972 USDI rodent poison guidelines.

BIGGINS, D. E., M. H. SCHROEDER, S. C. FORREST, AND L. RICHARDSON. 1986. Activity of radio-tagged black-footed ferrets. Great Basin Nat. Mem. 8:135–140.

Results of radio tagging studies of Wyoming BFFs are described.

BIGGINS, D. E., M. H. SCHROEDER, S. C. FORREST, AND L. RICHARDSON. 1985. Movements and habitat relations of radio-tagged black-footed ferrets. Pages 11.1–11.17 *in* S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.

Movements of four radio-tagged BFFs were monitored during the falls of 1981 and 1982. Lengths of movements are described and areas of activity characterized.

BISAILLON, A. 1975. La musculature du membre pelvien du putois d'Amerique (*Mustela nigripes*, Audubon et Bachman). Anat. Anz. 139:486–504.

Dissection of muscles of the pelvic limb of BFF. Musculature found to be very similar to other mustelids.

BISHOP, N. 1972. Black-footed ferret and black-tailed prairie dog survey, 1972. Unpubl. U.S. Forest Serv., Medora Ranger Dist., Dickinson, North Dakota. 21 pp.

Inventory of prairie dog colonies in 3 southwestern North Dakota counties.

BISSEL, S. J. 1979. Black-footed ferret verification and habitat inventory, June 17, 1977–September 30, 1978. Unpubl. rept., Colorado Div. Wildl., Denver. 15 pp.

BLACK-FOOTED FERRET FOUND; PUPFISH EXTINCT. 1981. Sci. News 120:340.

1981 Wyoming BFF find reported. Photo.

BLAIR, W. F. 1954. Mammals of the Mesquite Plains biotic district in Texas and Oklahoma, and speciation in the central grasslands. Texas J. Sci. 6:235–264.

A three-line note claims BFFs are very rare or extirpated in the Mesquite Plains district.

BODDICKER, M. L. 1968. Parasites of the black-footed ferret. Proc. South Dakota Acad. Sci. 47:141–148.

Fleas, ticks, nematodes, and mites were identified.

BOGAN, M. A. 1985. Needs and directions for future black-footed ferret research. Pages 28.1–28.5 *in* S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.

Two objectives are suggested: reconstitution of an advisory board to oversee BFF research and management, including more research representation, and important research topics, including basic ecology of Meeteetse BFFs, mortality factors, survey techniques, captive breeding and translocation, and prairie dogs.

BOGGESS, E. K., F. R. HENDERSON, AND J. R. CHOATE. 1980. A black-footed ferret from Kansas. J. Mammal. 61:571.

The skull and left mandible of a subadult male BFF were found in Gove County, Kansas, in November 1978, representing the first of the species found in the state in over 20 years.

BREWSTER, W. G. 1985. Black-footed ferret conservation and recovery from a Fish and Wildlife Service Field Office perspective. Pages 29.1–29.4 *in* S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.

Calls for implementation of six strategies: (1) conserve existing population, (2) continue research and monitoring, (3) initiate captive propagation for future release, (4) continue search for other populations, (5) evaluate and identify future reintroduction sites, and (6) develop complete management plans for reintroduction sites and subject them to public review.

BRIGHAM, E. M., III. 1973. The black-footed ferret: the view of a conservation organization. Pages 24–26 *in* R. L. Linder and C. N. Hillman, eds., Proc. Black-footed Ferret and Prairie Dog Workshop, South Dakota State University, Brookings.

Audubon Society representative suggests "prairie dog bank" or colony leasing program to preserve faunal community. Example of pro- and anticaptive breeding polarization.

BURNETT, W. L. 1918. Rodents of Colorado in their economic relation. Off. State Entom. Circ. 25. Fort Collins, Colorado. 31 pp.

BURT, W. H., AND R. P. GROSSENHEIDER. 1964. A field guide to the mammals. Field marks of all species found north of the Mexican boundary. 2d ed. Houghton Mifflin, Boston. 284 pp.

Resume of BFF with weights of two adults.

CADA, J. D. 1985. Montana's role in ferret management and handling of ferret sightings. Pages 14.1–14.7 *in* S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.

Montana Department of Fish, Wildlife and Parks initiated a program with the ultimate goal of recovering BFFs in the state. Discussion includes agency cooperation and future plans. Appendices provide observation report form and follow-up procedures.

CAHALANE, V. H. 1954. Status of the black-footed ferret. J. Mammal. 35:418–424.

Reviews status of BFF and reports 50–70 animals from 42 sightings from a canvass of federal employees from 1948 to 1953. Range map based on reports included. States that complacency regarding BFF is unjustified.

CAMPBELL, T. M., III, D. E. BIGGINS, S. FORREST, AND T. W. CLARK. 1985. Spotlighting as a method to locate and study black-footed ferrets. Pages 24.1–24.7 *in* S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.

The use of spotlighting as a search and research method, historically and in present day, is discussed. Results of a pilot study to assess BFF responses to this technique are presented.

CARAS, R. A. 1967. North American mammals. Meredith, New York. 578 pp.

Brief popular account of characteristics and life history with tips for finding and observing BFFs, "surely . . . the last one you tick off on your lifetime checklist."

CARPENTER, J. W. 1977. Propagation and management of endangered species at the Patuxent Wildlife Research Center. Proc. Amer. Assoc. Zoo Vet. 1977:23–33.

An introduction to the research and propagation techniques of the Endangered Wildlife Research Program. Electro-ejaculation and artificial insemination used on surrogate species of ferrets are potential methods for use with BFFs.

———. 1985. Captive breeding and management of black-footed ferrets. Pages 12.1–12.13 *in* S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.

A captive breeding program was conducted at the Patuxent Wildlife Research Center from 1968 to 1979. Results of this effort are reviewed and prognosis for successful future programs discussed along with role of captive breeding as adjunct to habitat preservation, field studies, law enforcement, and public education.

CARPENTER, J. W., M. J. G. APPEL, R. C. ERICKSON, AND M. N. NOVILLA. 1976. Fatal vaccine-induced canine distemper virus infection in black-footed ferrets. J. Amer. Vet. Med. Assoc. 169:961–964.

Four wild-captured BFFs held at Patuxent Wildlife Research Center died within 21 days after vaccination with modified canine distemper virus.

CARPENTER, J. W., J. D. DAVIDSON, M. N. NOVILLA, AND J. C. M. HUANG. 1980. Metastatic, papillary cystadenocarcinoma of the mammary gland in a black-footed ferret. J. Wildl. Dis. 16:587–592.

Decline and death of female BFF held at Patuxent Wildlife Research Center. Individual was captive from 1972–1973 to 1978. Includes necropsy and histological findings.

CARPENTER, J. W., AND E. F. HILL. 1979. Hematological values for the Siberian ferret (*Mustela eversmanni*). J. Zoo. An. Med. 10:126–128.

Baseline hematologic and blood chemistry values for the Siberian ferret may serve as reference for the physiological and pathological conditions of the BFF.

CARPENTER, J W., AND C. N HILLMAN. 1979. Husbandry, reproduction, and veterinary care of captive ferrets. Proc. Amer. Assoc. Zoo Vet., Knoxville, Tenn. 1979:36–47

Hundreds of European and Siberian ferrets held at the Patuxent Wildlife Research Center served as research surrogates for BFFs. The health of several wild-caught BFFs is discussed. Many husbandry, breeding, and surgical techniques were developed, and captive breeding may succeed if younger, genetically healthy BFFs are used.

CARPENTER, J. W., AND M. N NOVILLA. 1977. Diabetes mellitus in a black-footed ferret. J. Amer. Vet. Med. Assoc. 171:890–893.

A case report of diabetes mellitus in a BFF is followed by necropsy and histopathologic findings. This condition may have implications for any remnant population in the wild.

CARPENTER, J W., M. N. NOVILLA, AND H. E. KAISER. 1981. Neoplasia and other disease problems in black-footed ferrets: implications for an endangered species. Pages 739–746 *in* H. E. Kaiser, ed., Neoplasms: comparative pathology of growth in animals, plants, and man. Raven Press, New York.

Examines neoplasia and concurrent disease conditions in five captive BFFs and suggests that their origin is associated with genetic homozygosity resulting from inbreeding.

CARR, J. F 1973. A rancher's view towards prairie dogs. Pages 168–171 *in* R. L. Linder and C. N. Hillman, eds., Proc. Black-footed Ferret and Prairie Dog Workshop, South Dakota State University, Brookings.

Wyoming rancher's insight into the sources of social/political conflict between preservationists, agencies, and private landowners.

CARY, N. 1911. A biological survey of Colorado. U.S. Biol. Surv. North Amer. Fauna No. 33. U.S. GPO, Washington, D.C. 256 pp.

Maps BFFs in plains of Colorado. States that they are most beneficial because they prey on prairie dogs.

CHACE. G E. 1960. The Recent mammals of Arizona: their taxonomy and distribution. University of Arizona Press, Tucson. 276 pp.

———. 1973. Prairie dogs, ferrets, and cattle—conflict on the plains. Anim. Kingdom 76(2):2–8.

Different perceptions of the role of prairie dogs in ecosystems affects the survival of both *Cynomys* and *M. nigripes*. Basic review of BFF life history, behavior, and habitat loss dilemma.

CHARLES. G. 1965. Will they survive? South Dakota Conserv. Dig. 32(2):6–8.

CHOATE. J. R., E. K BOGGESS. AND F. R HENDERSON. 1982. History and status of the black-footed ferret in Kansas. Trans. Kansas Acad. Sci. 85:121–132.

The BFF was probably common in certain areas of Kansas west of the Flint Hills. Twenty-eight of 38 museum specimens from the state were collected before 1900, and most were males. Agriculture and prairie dog control blamed for demise of the BFF.

CLARK. T W. 1973. Prairie dogs and black-footed ferrets in Wyoming. Pages 88–101 *in* R. L. Linder and C. N. Hillman, eds., Proc. Black-footed Ferret and Prairie Dog Workshop, South Dakota State University, Brookings.

Attempt to inventory prairie dogs and BFFs. Author reports on a mail survey for BFFs and prairie dogs in Wyoming. Lists and maps of black- and white-tailed prairie dog colonies and BFF locations in 1971 and historical times.

———. 1974a. "Black-footed ferrets"—searching for America's rarest mammal. Cow Country, May:28.

A one-page introduction to the BFFs appearance and habits, history of search efforts in Wyoming, and a plea for information.

———. 1974b. Ferrets—are there any left in Wyoming? Wyoming Agric., April:6–7.

A quick introduction to the BFF and its sign with a request for information.

———. 1974c. Vanishing bandits of the prairie. Wyoming Wildl. 38(6):32–33.

Outlines history of BFFs in Wyoming leading up to 1974d campaign to record recent sightings.

———. 1974d. A vanishing friend. Wyoming Rural Electric News, April:10.

Yet another introduction to the BFF, part of the author's early 1970's campaign to publicize BFFs and gather information.

_____. 1975a. Wyoming's search for black-footed ferrets. Wyoming Rural Electric News, September: 10–11.

Another introduction to the species, this time focusing on sightings and remains that were turned up by the author's "Ferret Search."

_____. 1975b. Some relationships between prairie dogs, black-footed ferrets, Paleo-Indians and ethnographically known tribes. Plains Anthrop. 20–67: 71–74.

Fifteen BFF remains found at one Paleo-Indian site in Wyoming. BFFs used as religious objects and head-dress pendants.

_____. 1976. The black-footed ferret. Oryx XIII:275–280.

Popular account of historical and ecological details of BFFs.

_____. 1978a. Current status of the black-footed ferret in ming. J. Wildl. Manage. 42:128–133.

Review of BFF reports in Wyoming, hypotheses about BFF decline, and methods of searching for populations. Recommends prairie dog management techniques for BFF preservation, including termination of control on all colonies suspected of supporting BFFs.

_____. 1978b. Losing the ferret. Defenders Wildl., January:245–248.

Discussion of conflicting agency responsibilities toward BFFs. Lack of information on prairie dog control makes it hard to assess status of BFF. New location techniques are necessary.

_____. 1980. A listing of reports of the black-footed ferret in Wyoming (1851–1977). Northwest Sci. 54: 47–54.

Lists and evaluates 148 Wyoming BFF reports. The increasing number of reports in recent years is the result of increased concern for the BFF, not an indication of increased abundance.

_____. 1982. Status of the rare and endangered black-footed ferret in Wyoming. Natl. Geog. Soc. Res. Rept. 14:95–105.

145 valid BFF sightings in Wyoming were collected during a search effort in 1973–1975 resulting from a publicity campaign throughout the state. Evaluation criteria are given; a map shows locations of reports. Concludes that the existence of BFFs is verified.

_____. 1983. Last of the black-footed ferrets? Natl. Geog. 163:828–838.

A short popular account of some highlights of the first year's research on Wyoming BFFs. Many excellent photos.

_____. 1984a. Biological, sociological and organizational challenges to endangered species conservation: the black-footed ferret case. Human Dimensions in Wildl. Newsletter 3:10–15.

Outlines problems on several fronts that must be overcome to set up successful conservation programs.

_____. 1984b. Strategies in endangered species conservation: research view of the ongoing black-footed ferret conservation studies. Pages 145–154 in Symposium on Issues in Technology and Management of Impacted Western Wildlife, Steamboat Springs, Colorado, November, 1982.

As a step toward developing a case history, the role of the private research arm of the Wyoming BFF program is presented. The historic role of the conservation community in wildlife protection, management, and study is reviewed, and some ideas for achieving model conservation programs are brought together.

_____. 1985a. The Meeteetse black-footed ferret conservation studies. Natl. Geog. Res.:299–302.

Reports progress in a study "directed toward those parameters of ferret-prairie dog relationships which are significant for the conservation of the ferret."

_____. 1985b. Black-footed ferret studies in Wyoming. Natl. Geog. Res. 18:223–231.

Search efforts in Wyoming in 1979 are reported, the environments around 10 reported BFF sightings are described, and BFF habitat is discussed.

_____. 1986. Some guidelines for management of the black-footed ferret Great Basin Nat. Mem. 8: 160–168.

Specific management guidelines for monitoring and protecting the Wyoming BFF and its habitat are given. The BFFs current status and all the primary baseline data sources and methods are identified.

CLARK, T. W., AND T. M. CAMPBELL III. 1981a. Additional black-footed ferret (Mustela nigripes) reports from Wyoming. Great Basin Nat. 41:360–361.

39 BFF sightings added to Clark 1980. Addendum reports 26 September 1981, dog-killed BFF from Park County, Wyoming.

_____. 1981b. Suggested guidelines for black-footed ferret surveys. Printed by the authors, Biota Research and Consulting, Inc., Box 2705, Jackson, Wyoming 83001.

State-of-the-art description of field survey techniques. Recovery team reviewed these guidelines and declared them adequate. Introduces a method for comparing intensity of nocturnal searches.

_____. 1983. A small carnivore survey technique. Great Basin Nat. 43:438–440.

A track station survey method has implications for BFF surveys.

CLARK, T. W., T. M. CAMPBELL III, M. H SCHROEDER, AND L. RICHARDSON. 1984. Handbook of methods for locating black-footed ferrets. Wyoming Bur. Land Manage. (Cheyenne) Wildl. Tech. Bull. No. 1. 55 pp.

Detailed methods for conducting BFF surveys. Discusses general life history and BFF sign. Photos of BFFs, diggings, tracks, scats. Appendices include reprints of Hillman and Clark 1980 and Fortenbery 1972, additional references, a key to mustelid skulls, and a postcranial comparison of the prairie dog and BFF.

CLARK, T. W., S. C. FORREST, L. RICHARDSON, D. E. CASEY, AND T. M. CAMPBELL III. 1986. Description and history of the Meeteetse black-footed ferret environment. Great Basin Nat. Mem. 8:72–84.

Climate, soils, and vegetation of the BFF-occupied area are described along with a history of ranching, poisoning, and grazing. The area contains evidence of a historically larger prairie dog complex.

CLARK, T. W., L. RICHARDSON, D. CASEY, T. M. CAMPBELL III, AND S. C. FORREST. 1984. Seasonality of black-footed ferret diggings and prairie dog burrow plugging. J. Wildl. Manage. 48:1441–1444.

Configuration, rate of production, persistence, and seasonality of BFF diggings and prairie dog burrow plugging patterns on white-tailed prairie dog colonies are described based on a two-year sample. The results have implications for timing and "search images" of prescribed BFF and BFF-sign searches.

CLARK, T. W., L. RICHARDSON, S. C. FORREST, T. M. CAMPBELL III, D. E. CASEY, AND K. A. FAGERSTONE. 1985. Black-footed ferret prey base. Pages 7.1–7.14 in S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.

The BFF-occupied prairie dog complex totals about 3,000 ha in 33 colonies; the Big Horn Basin has 40,485 ha in 250 colonies, and the state has an estimated 6,000 colonies. Ferret/prairie dog computer models are reviewed and recommendations made for transplants and captive breeding.

CLARK, T. W., L. RICHARDSON, S. C. FORREST, D. E. CASEY, AND T. M. CAMPBELL III. 1986. Descriptive ethology and activity patterns of black-footed ferrets. Great Basin Nat. Mem. 8:115–134.

Observations of BFFs between December 1981 and September 1984 included ferret maintenance behaviors (locomotion, alert, grooming and sunning, defecation and urination, digging, and predation) and social behaviors (reproduction, ontogeny, maternal, play, and agonistic).

CLARK, T. W., AND J. L. WEAVER. 1981. Mammals. Pages 50–64 in T. W. Clark and R. D. Dorn, eds., Rare and endangered vascular plants and vertebrates of Wyoming, 2d ed. Offset. 66 pp.

Account of distinguishing characteristics, habitat, present and former distribution, reasons for decline, and legal status of BFF.

COCKRUM, E. L. 1952. Mammals of Kansas. Univ. Kans. Mus. Nat. Hist. Publ. 7:1–303.

BFF distributed in western half of Kansas.

COLLINS, E., AND R. W. LICHVAR. 1986. Vegetation inventory of current and historic black-footed ferret habitat in Wyoming. Great Basin Nat. Mem. 8:85–93.

Prairie dogs occur in two of eight vegetation types in the BFF-occupied area (junegrass and sagebrush/junegrass), whereas four other prairie dog complexes with historic BFF occupancy occurred in six vegetation types. Similarities of the five complexes were plant heights < 66 cm, level to gently rolling topography, and severe human-caused disturbance. Conclusion that vegetation type alone should not be used to identify BFF habitat.

CORBET, G. B. 1978. The mammals of the Palearctic Region: a taxonomic review. British Museum and Cornell University Press, New York. 314 pp.

Mentions that *M. eversmanni* is considered conspecific with BFF.

CORDER, R. L. 1968. The black-footed ferret. Natl. Parks 42:7–8.

BFF considered third rarest animal in America. Populations declined along with prairie dogs. General overview; asks for reports.

COUES, E. 1874. Wanted. Amer. Sportsman 5:1.

Calls for specimens of BFF to benefit science.

_____. 1877. Fur-bearing animals: a monograph of North American Mustelidae. U.S. Geol. Surv. of the Territories, Misc. Publ. No. 8. U.S. GPO, Washington, D.C.

Contrary to other accounts, the BFF was not rare on the prairie. Created a new subgenus for BFF based on skull characteristics. The earliest "full account" of the species based on examination of several specimens, some in response to his advertisements for specimens. Describes distribution (expected to be enlarged) and detailed body characteristics. Notes that "its retiring habits, and the nature of its resorts, doubtless tend(ed) to screen it" despite extensive exploration of the West.

_____. 1882. The black-footed ferret (*Putorius nigripes*) in Texas. Amer. Nat. 16:1009.

BFF captured near Abilene, Texas, in 1882 is placed on exhibition at Cincinnati Zoological Gardens. The specimen expands the known range in Texas. Called a "rare species."

CRABB, W. D., AND G. W. WATSON. 1950. Black-footed ferret in Montana. J. Mammal. 31:99.

Lists two BFF occurrences in southcentral Montana during 1948–1949. One specimen was road killed, the other shot in a prairie dog town.

CRAGIN, F. W. 1885. Notes on some mammals of Kansas, with a few additions to the list of species known to inhabit the state. Bull. Washburn College Lab. Nat. Hist. 1:42–47.

CRANDELL, L. S. 1964. The management of wild mammals in captivity. University of Chicago Press, Chicago. 761 pp.

Information on BFF feeding trials.

CRETE, R. 1985. Current activities of the U.S. Fish and Wildlife Service in black-footed ferret recovery management. Pages 15.1–15.6 *in* S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.

Outlines FWS responsibility in implementation of recovery plans, including responses to sightings, training programs, formulating criteria to identify recovery areas, survey methods, law enforcement, etc.

DALQUEST, W. W. 1968. Mammals of northcentral Texas. Southwest. Nat. 13:13–21.

DARTT, M. 1879. On the plains, and among the peaks; or, How Mrs. Maxwell made her natural history collection. Claxton, Remsen and Hffelfinger, Philadelphia. 237 pp.

A woman naturalist and taxidermist had two or three BFFs in her collection, confirmed by Coues. They were drowned out of prairie dog burrows or trapped. She kept one captive, fed it beef, and kept it in a wire cage, where it was active at night. It became quite tame.

DAY, A. M., AND A. P. NELSON. 1929. Wildlife conservation and control in Wyoming under the leadership of the United States Biological Survey. Joint Pub. U.S. Biol. Surv., Wyoming Game Fish Dept., Wyoming State Extension Serv., Wyoming Dept. Agric. Wyoming State Hist. Pub. 26 pp.

Ten BFFs taken in predator control activities in state between 1916 and 1928.

DEXTER, W. D. 1985. Introductory remarks. Pages 1.1–1.2 *in* S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.

Defines purpose of meeting to review status of searches, research, and management with 35 invited scientists. Reviews establishment of advisory team to provide department with broad input to research and management and ad hoc committee to evaluate captive breeding facilities.

DIXON, L., M. H. SCHROEDER, AND S. J. MARTIN. 1980. A serious game of hide and seek. Wyoming Wildl. XLIV(6):12–15.

Overview of BFF ecology and history. 1978 and 1979 Wyoming coal lease surveys yielded six BFF skulls but no live BFFs. Techniques included dogs and winter helicopter and snowmobile searches. Three more years of searches are planned for four likely areas based on historical and recent evidence.

DOHERTY, J. G. 1970. Black-footed ferret. Anim. Kingdom 73(1):33.

Brief review of *Mustela nigripes* plight. Suggests protection of both prey and habitat. Photo of zoo-held animal.

DURRANT, S. D. 1952. Mammals of Utah: taxonomy and distribution. University of Kansas Mus. Nat. Hist. Publ. No. 6. 549 pp.

Brief account listing single specimen for state; states that species was not expected to be found north of the Colorado River.

EMERSON, K. C. 1964. Checklist of the Mallophaga of North America (north of Mexico). Pt. 1. Sub-order Ischnocera. Dugway Proving Ground, Dugway, Utah. 171 pp.

Lists the louse *Neotrichodectes minutus* as a BFF parasite.

ERICKSON, R. C. 1968. A federal research program for endangered wildlife. Trans. North Amer. Wildl. Nat. Resour. Conf. 33:418–433.

Description of Patuxent Wildlife Research Center's responsibility for "technical investigation and propagation of rare and endangered species." BFF considered one of the priority species. Applications toward improved survey techniques, ensuring adequate precontrol surveys. Mentions disease as captive-breeding problem; for BFF, rabies, distemper, and tularemia are major concerns.

_____. 1973. Some black-footed ferret research needs. Pages 153–164 *in* R. L. Linder and C. N. Hillman, eds., Proc. Black-footed Ferret and Prairie Dog Workshop, South Dakota State University, Brookings.

Discusses research needs: increasing animal reproductions, survival and population in historical range. Brief sections on BFF populations and distributions, mobility and spatial requirements, behavioral and biological characteristics, vertebrate associates, and development of management practices.

ETTER, A. G. 1965. How to endanger a ferret. Defenders Wildl. News 40(4):30–38.

Popular description of BFF and prey relations. Links bison, cattle, prairie dogs, and BFF. Description of pest control vs. endangered species program politics.

FAGERSTONE, K. A. 1986. Comparison of capture-recapture and visual count indices of prairie dog densities in black-footed ferret habitat. Great Basin Nat. Mem. 8:94–98.

Prairie dog surveys in the Meeteetse area are described along with recommended procedures for surveys in areas being assessed for BFF transplant sites.

FAGERSTONE, K. A., D. E. BIGGINS, AND T. M. CAMPBELL III. 1985. Marking and radio-tagging of black-footed ferrets (*Mustela nigripes*). Pages 10.1–10.10 *in* S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.

The history of the development of marking and radio-tagging techniques by the Denver Wildlife Research Center is reviewed, and current techniques described.

FICHTER, E., AND J. K. JONES, JR. 1953. The occurrence of the black-footed ferret in Nebraska. J. Mammal. 34:385–388.

Review of Swenk's (1908) Nebraska BFF records, most from the southcentral loess plains. Range map.

FISHER, J., N. SIMON, AND J. VINCENT. 1969. Wildlife in danger. Viking Press, New York.

Synopsis of BFF as an endangered species. Mentions agency efforts to manage species.

FLATH, D. L., AND T. W. CLARK. 1984. Montana: crucial key to ferret recovery. Montana Outdoors 15(3):34–37. Reprinted in Defenders 59(5) (September-October):30–34.

General history of ferrets and search techniques focusing on Montana. State Department of Fish, Wildlife, and Parks decision to search for ferrets in Montana and its implications for the agriculture and livestock industries.

_____. 1986. Historic status of black-footed ferret habitat in Montana. Great Basin Nat. Mem. 8:63–71.

Northern Pacific Railroad lands were surveyed 1908–1914 (just prior to widespread prairie dog poisoning). Of 6,661 sections in 22 counties in Montana, 1,662 (25%) contained some prairie dogs. Totaling a minimum of 47,568 ha in 1914, prairie dog colonies have been reduced in the area by 90+%. Implications for BFFs and their possible reintroduction are discussed.

FORREST, S. C., T.W. CLARK, L. RICHARDSON, D. BIGGINS, K. A. FAGERSTONE, AND T. M. CAMPBELL III. 1985. Life history characteristics of the genus *Mustela*, with special reference to the black-footed ferret, *Mustela nigripes*. Pages 23.1–23.14 *in* S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.

Common attributes of 10 mustelids are high turnover rates, high juvenile mortality, and low average life spans (< 1 yr). BFFs bear 3.38 young/year, exhibit equal juvenile sex ratios, and females breed and bear young at one year of age. High annual declines have been observed.

FORREST, S. C., T. W. CLARK, L. RICHARDSON, AND T. M. CAMPBELL III. 1985. Black-footed ferret habitat: some management and reintroduction considerations. Wyoming Bur. Land Mgmt. Wildl. Tech. Bull. No. 2, Cheyenne. 49 pp.

FORTENBERY, D. K. 1969. Green eyes and a mask—seen any lately? Insight, November:1,4.

_____. 1972. Characteristics of the black-footed ferret. U.S. Fish and Wildl. Serv. Resour. Publ. 109. 8 pp.

Good semitechnical review of BFF characteristics and ecology. Good comparison with congeners. Illustrations of scats, trenches, and congeners.

FRARY, L. G. 1985. Black footed ferret/prairie dog management on national forest system lands. Pages 16.1–16.6 *in* S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.

Discusses policies for prairie dog management and control and BFF surveys and sightings on national forests and national grasslands.

GARST, W. E. 1954. Black-footed ferret in South Dakota. J. Mammal. 35:594.

Six BFFs located by government employees following prairie dog poisoning in Haakon County. Litter of 5 captured: 2 died, 3 released in Wind Cave National Park.

GEORGE, J. 1969. From the brink of extinction: endangered wildlife research program. Nat. Wildl. 7:20–23. (Reprinted Read. Dig. 94:214–218.)

Review of research activities of the Endangered Species Research Program since its inception in 1965. Brief mention of BFF captive propagation program.

GETZ, L. L. 1960. Middle Pleistocene carnivores from southwestern Kansas. J. Mammal. 41:361–365.

GILBERT, B. 1980. Missing amd presumed to be dead. Sports Illus. 53(16):102–114.

Popular account of the politics of the BFF leading to its "de-emphasis" by federal officials in 1980.

GORDON, C. 1965. Our vanishing species: will they survive? South Dakota Conserv. Dig. 32(2):6–8.

GRAY, J. E. 1865. Proceedings of the Zool. Soc., p. 110.

Lists species and mentions that it was not seen by S. Baird. The single question mark indicating the author's doubting the existence of the species set off a decade-long controversy.

GRINNELL, G. B. 1895. The story of the Indian. D. Appleton Co., New York. 270 pp.

Nebraska Pawnees believed BFFs had supernatural power and were able to kill men.

———. 1896. Range of the black-footed ferret. Forest and Stream 47(5):84.

A letter in response to Merriam's *Synopsis of the weasels of North America* extends the range north in Montana, to the foothills of the Rockies, and to the Continental Divide Basin in Wyoming. Includes personal observations, Indian accounts, and some life history information for BFFs.

GRODE, M. R. 1985. The black-footed ferret in Colorado. Pages 17.1–17.4 *in* S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.

Reviews historic records and Division of Wildlife processing of reports. Although there is no current BFF project, preliminary work in summer spotlighting, winter ground searches, and prairie dog mapping has begun. A BFF scat was positively identified in 1983.

GRONDAHL, C. R. 1973. Status of the black-tailed prairie dog and the black-footed ferret in North Dakota. Pages 51–60 *in* R. L. Linder and C. N. Hillman, eds., Proc. Black-footed Ferret and Prairie Dog Workshop, South Dakota State University, Brookings.

BFF habitat restricted to southwestern North Dakota. Lists by county the number of towns and acreages of black-tailed prairie dogs and BFF sightings from 1910 to 1973. No recent "verified" reports.

GROVES, C. R., AND T. W. CLARK. 1986. Determining minimum population size for recovery of the black-footed ferret. Great Basin Nat. Mem. 8:150–159.

Minimum viable population size is estimated by five methods: experiments, biogeographic patterns, theoretical models, simulation models, and genetic considerations. Genetic factors suggest a MVP of about 200 BFFs for short-term fitness. Implications for research, management, and recovery efforts.

HAILEY, D. 1978. The weasel tribe. Defenders 53: 265–272.

General review of mustelid and BFF life history.

HALL, E. R. 1951. American weasels. University of Kansas Publ. Mus. Nat. Hist. 466 pp.

Standard reference to weasel life history.

———. 1966. The endangered black-footed ferret. Defenders Wildl. News 41:109.

———. 1981. Mammals of North America, 2d ed., 2 vol. John Wiley and Sons, New York. 1,181 pp.

Technical account of characteristics, distribution, and taxonomy. Includes drawings of animal and skull, and a range map.

HALLORAN, A. F. 1950. The black-footed ferret. Arizona Wildl.-Sport. 11(10):9.

———. 1964. The mammals of Navajoland. Navajo Tribal Mus., Window Rock, Arizona. 23 pp.

Brief description with two reports from Navajoland from 1936 and 1940. The Navajo name is "dlo'ii liz-hinii," meaning black weasel.

HAMMER, D. A. 1985. The handling of black-footed ferret sighting reports in Wyoming. Pages 18.1–18.4 *in* S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.

Historic records of BFFs in Wyoming are noted. Report handling consists of detailed interviews, possible site visits and searches, and departmental filing.

HAMMER, D. A., AND S. H. ANDERSON. 1985. Using scent attractants as a technique to locate black-footed ferrets. Pages 26.1–26.12 *in* S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.

Sixteen scent attractants were evaluated as BFF lures in the lab, and six were subsequently evaluated in the field in known BFF-occupied areas. No BFF visitations were documented.

HARDING, A. R. 1943. Ferret fact and fancies. A. R. Harding Publ. Co., Columbus, Ohio. 214 pp.

Aspects of fitch ferret life including diseases pertinent to BFFs.

HARJU, H. J. 1985a. Black-footed Ferret Advisory Team efforts. Pages 4.1–4.4 *in* S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.

The advisory team was created to oversee BFF work in an area of varied land and management jurisdiction. Representing management agencies and private concerns, it has reviewed research-management and information education plans, reviewed and approved research, sought funding for research, mediated BFF-development conflicts, and maintained control of all BFF-related activities in the state.

_____. 1985b. Needs for black-footed ferret research and management: Wyoming Game and Fish Department perspectives. Pages 30.1–30.4 *in* S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.

Research needs include additional data on movements, dispersal, and mortality, and evaluation of potential transplant sites, captive breeding techniques, and search techniques. Management needs include finding BFFs, enhancing habitat or mitigating its loss, dealing with BFF/mineral development conflicts and prairie dog control, and conducting public relations campaigns.

HARVEY, L. 1970. Black-footed (*Mustela nigripes*); a bibliography. Bibliog. Ser., USDI. No. 17. 23 pp.

Bibliography of BFF literature organized to assist wildlife management personnel. Includes ecology, life history, history of man's interactions. Also includes geographic index and layman's reading list.

HASENYAGER, R. 1985. Utah's ferret program–past, present and future. Pages 19.1–19.2 *in* S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.

The Utah Division of Wildlife Resources has improved its network for receiving, investigating, and recording BFF sightings, plans intensive surveys of 2 areas, and seeks guidelines for dealing with the discovery and management of BFFs.

HASSIEN, F. D. 1976. A search for black-footed ferret in the Oklahoma Panhandle and adjacent area and an ecological study of black-tailed prairie dogs in Texas County, Oklahoma. Unpublished thesis Oklahoma State University, Stillwater.

HAYDEN, F. V. 1863. On the geology and natural history of the Upper Missouri. Part 3. Zoology and botany. Chapter 15, Mammals. Trans. Amer. Phil. Soc. 12:138–151.

Mentions skin examined and described by Audubon and Bachman from Fort Laramie.

HENDERSON, F. R. 1966. Watching I Top Ta Sap A. South Dakota Conserv. Dig. 33(5):16–18.

_____. 1968. Ferret search on in Kansas. Kansas Fish and Game 26(1):18–21.

Overview of BFF ecology with distribution and abundance in Kansas. Good photographs of BFFs and winter trench.

_____. 1969. Wanted: Black-footed ferret. Coop. Ext. Serv., Kansas State University, Manhattan. 8 pp.

HENDERSON, F. R., AND R. J. LITTLE. 1973. Status of the black-footed ferret and black-tailed prairie dog in Kansas. Pages 34–40 *in* R. L. Linder and C. N. Hillman, eds., Proc. Black-footed Ferret and Prairie Dog Workshop, South Dakota State University, Brookings.

Most BFF sightings of recent decades were in the western half of Kansas. Most recent specimen captured in 1957. In 1969–1970 state searched for BFFs through a media campaign and follow-up field investigations. BFF listed as extirpated by the Soil Conservation Service and Kansas Academy of Science in 1973.

HENDERSON, F. R., R. F. SPRINGER, AND R. ADRIAN. 1969. The black-footed ferret in South Dakota. South Dakota Dept. Game, Fish and Parks Tech. Bull. No. 4. 37 pp.

Government document on all aspects of BFFs, resulting from study of the Mellette County, South Dakota, population. Study had three goals: (1) determination of distribution and status of South Dakota BFFs, (2) gathering of life history, behavioral and ecological data, and (3) development of location techniques.

HERMAN, M., AND E. E. WILLARD. [1977]. Black-footed ferret and its habitat. Montana For. Conserv. Expt. Sta., U.S. For. Serv. 24 pp.

Summary of BFF historical distribution, present status, and habitat relationships. Primarily a literature review. Includes extensive reference section by subject and a conceptual model of BFF habitat.

HERSHKOVITZ, P. 1966. Status of the black-footed ferret in Wyoming. J. Mammal. 47:346–347.

Close-range sighting of BFF crossing highway east of Casper, Wyoming.

HIBBARD, C. W. 1934. The occurrence of *Erethizon epixanthum* Bruneri and *Mustela nigripes* in Kansas. J. Mammal. 15:70–71.

Notes that BFF had not been seen in the state for many years but reports a road-killed specimen from 1930 was mounted and given to the university museum.

_____. 1944. A checklist of Kansas mammals, 1943. Trans. Kans. Acad. Sci. 47:61–88.

"Due to the destruction of most of the prairie-dog towns in Kansas the Black-footed Ferret is now on the verge of extinction in the State."

HILL, E. F., AND J. W. CARPENTER. 1982. Responses of Siberian ferrets to secondary zinc phosphide poisoning. J. Wildl. Manage. 46:678–685.

Zinc phosphide-poisoned rats were fed to 16 Siberian ferrets (*Mustela eversmanni*). Ferrets accepted rats and 3 individuals had an emetic response to the toxin. Authors conclude that emetic reflex protects carnivores against zinc phosphide poisoning but state the necessity of secondary "safe" prey items following poisoning of primary prey.

HILLMAN, C. N. 1968a. Field observations of black-footed ferrets in South Dakota. Trans. North Amer. Wildl. Nat. Resour. Conf. 33:433–443.

Results of 1966–1967 field study of BFF population in Mellette County, southwestern South Dakota. Data on diurnal activity, reproduction, and mother/young behavior; food habits and dispersal; behavioral response of *Cynomys* to BFFs. Description of BFF sign. Domestic ferret (*Mustela putorius*) 1080 feeding experiment.

———. 1968b. Life history and ecology of the black-footed ferret in the wild. Unpublished thesis, South Dakota State University, Brookings. 28 pp.

Field observations revealed activity patterns, behavior, movements, food habits, and BFF/prairie dog relationships.

———. 1974. Status of the black-footed ferret. Pages 75–81 *in* Symposium on Endangered and Threatened Species of North America Proceedings. Wild Canid Survival and Research Center, St. Louis, Missouri.

A solid review of the South Dakota research on BFF life history, past and present distribution, and current programs and problems. Noteworthy is the insight that "observational" efforts are not providing answers needed for effective management.

HILLMAN, C. N., AND D. K. FORTENBERY. 1967. Field studies of the black-footed ferret in South Dakota. Wildlife Society, Central Mountains and Plains Section, 12th Annual Conf., Rapid City, South Dakota, 1967. Abstract (mimeograph).

An early report of the South Dakota studies giving observations of basic BFF distribution and ecology.

HILLMAN, C. N., AND R. L. LINDER. 1973. The black-footed ferret. Pages 10–23 *in* R. L. Linder and C. N. Hillman, eds., Proc. Black-footed Ferret and Prairie Dog Workshop, South Dakota State University, Brookings.

Synopsis of South Dakota BFF population work. Describes distribution, behavior, sign, BFF effects on prairie dogs, and research and management needs.

HILLMAN, C. N., R. L. LINDER, AND R. B. DAHLGREN. 1979. Prairie dog distributions in areas inhabited by black-footed ferrets. Amer. Midl. Nat. 102: 185–187.

Distribution of black-tailed prairie dog colonies in Mellette County, South Dakota, was examined to determine characteristics of BFF habitat. BFFs had been observed on 14 of 86 colonies in the study area. Management recommendations concerning size and distribution of colonies for BFFs are made.

HILLMAN, C. N., AND J. W. CARPENTER. 1980. Masked mustelid. Nature Conservancy News, March-April:20–23.

A good popular article describing the plight of the BFF, its life history, and captive breeding attempts in the 1970s, with mention of current location techniques and management efforts.

———. 1983. Breeding biology and behavior of captive black-footed ferrets. Intl. Zoo Yearbook 23:186–191.

The breeding biology and behavior of four wild-caught BFFs held at Patuxent Wildlife Research Center and studied 1975–1978 were similar to closely related mustelids. Reproductive disorders and other pathologic conditions were encountered.

HILLMAN, C. N., AND T. W. CLARK. 1980. *Mustela nigripes*. Mamm. Species No. 126. 3 pp.

Up-to-date technical synopsis of species.

HILLMAN, C. N., AND W. A. WENTZ. 1985. Private sector perspectives on needs and direction of ferret research and management. Pages 32.1–32.5 *in* S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.

Experiences with BFFs in South Dakota are applied to the Wyoming population. It is recommended that long-term funding be developed to maintain and enhance the species.

HINCKLEY, D. K., AND J. E. CRAWFORD. 1973. Ferret and prairie dog programs on the national resource lands. Pages 133–135 *in* R. L. Linder and C. N. Hillman, eds., Proc. Black-footed Ferret and Prairie Dog Workshop, South Dakota State University, Brookings.

Authors estimate 30 million acres of federal land are suitable for prairie dogs. Managing for prairie dogs is managing for BFFs. Mentions progress in search methods and inventorying of prairie dog colonies.

HOFFMANN, R. S., P. L. WRIGHT, AND F. E. NEWBY. 1969. The distribution of some mammals in Montana. I. Mammals other than bats. J. Mammal. 50: 579–604.

Lists state records for the BFF, the last in 1953.

HOMOLKA, C. L. 1964. Our rarest mammal? Audubon Mag. 66:244–246. (Reprinted 1965, The black-footed ferret, Oryx 8:105–106.)

Overview of rarest mammal and man's failure to refrain from habitat destruction.

———. 1967. This masked bandit is definitely on the nation's wanted list–wanted alive. Experts claim only 20 are left. Nebraskaland 45(8):53.

HOOGLAND, J. L. 1981. The evolution of coloniality in white-tailed and black-tailed prairie dogs (Sciuridae: *Cynomys leucurus* and *C. ludovicianus*). Ecology 62:252–272.

A six-year study indicated that reduced predation may be the most important benefit of prairie dog coloniality. Discusses the possible effect of nocturnal, burrow-entering BFF on prairie dogs compared to diurnal predators.

———. 1982. Reply to a comment by Powell, notes and comments. Ecology 63:1968–1969.

Debate over costs and benefits of coloniality in prairie dog species. Powell suggested that white-tails are less dense because their range overlaps less with BFF than black-tails. Hoogland answers cogently that the BFF range overlap with black-tails should be interpreted as an *effect* of greater colony density, not a cause.

HOOPER, E. T. 1941. Mammals of the lava fields and adjoining areas in Valencia County, New Mexico. University of Michigan Mus. Zool. Misc. Publ. No. 51. 47 pp.

HOUSTON, B., T. W. CLARK, AND S. MINTA. 1986. Habitat suitability index model for the black-footed ferret: a method to locate transplant sites. Great Basin Nat. Mem. 8:99–114.

An HSI model following the U.S. Fish and Wildlife Service model series assumes that BFFs can meet year-round habitat requirements within prairie dog colonies providing colonies are large enough, burrows are numerous enough, and adequate numbers of prairie dogs and alternate prey are available. Literature is reviewed and model assumptions and structure are discussed.

HUBBARD, J. P., AND C. G. SCHMITT. 1984. The black-footed ferret in New Mexico. Final report to BLM Santa Fe, New Mexico, under BLM Contract No. NM-910–CT1–7 to Dept. Game Fish, Santa Fe, and under New Mexico Dept. Game Fish Proj. FW-17–R.

A comprehensive summary of background information on BFFs and the status of both prairie dogs and BFFs in the state, with special emphasis on historic records and recent efforts to locate BFFs.

INTERNATIONAL UNION FOR CONSERVATION OF NATURE AND NATURAL RESOURCES. 1982. Black-footed ferret. Pages 349–351 *in* IUCN Red Data Book. Morges, Switzerland.

Excellent summary of BFF including brief discussion of ecology, threats to survival, conservation measures taken and proposed.

JOBMAN, W. G., AND M. E. ANDERSON. 1981. Potential present range of the black-footed ferret as of January 1, 1981. Unpubl. rept., U.S. Fish Wildl. Serv., Pierre, South Dakota. 65 pp.

———. 1985. Legal status and required action: ferret research and management. Pages 2.1–2.8 *in* S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.

A literature review of laws that affect BFF research and management revealed that the major law is the 1973 Endangered Species Act, although other laws have key significance when particular recovery actions are taken.

JOHNSON, D. 1969. Returns of the American Fur Company, 1835–1839. J. Mammal. 50:836–839.

Pelts of 86 BFFs were shipped in the fur trade during these years.

JOHNSON, M. K., T. W. CLARK, M. H SCHROEDER, AND L. RICHARDSON. 1986. Fecal bile acids of black-footed ferrets. Great Basin Nat. Mem. 8:135–140.

Fecal bile acids in scats of 20 BFFs, 7 other small carnivores, and 72 of unknown origin were analyzed to see if the method could be used to verify BFF presence. Substantial overlap among confidence intervals with other species led to the conclusion that the method is not useful. Gas-liquid chromatography is suggested instead.

JONES, J. K., JR. 1957. Checklist of mammals of Nebraska. Trans. Kansas Acad. Sci. 60:273–282.

Provides locations of BFFs collected in Nebraska, and states that BFFs are capable of decimating prairie dog populations.

———. 1964. Distribution and taxonomy of mammals of Nebraska. Publ. University of Kansas Mus. Nat. Hist. 16.

JONES, J. K., JR., AND R. B. LOOMIS. 1953. Additional records of the spotted ground squirrel and black-footed ferret in Kansas. Trans. Kansas Acad. Sci. 56:107.

Gives measurements of an unsexed adult BFF from 1944 and states that a few individuals may still inhabit the western part of Kansas.

KANSAS FISH AND GAME COMMISSION. (n.d.) Black-footed ferret investigations. Final report.

Field studies in Cheyenne County, Kansas, 1975–1977 yielded no live BFFs although one had been observed in 1975. A decline in BFF habitat was noted. Report suggests that, if captive breeding provides animals for recruitment, the hurdles of poisoning, harassment, shooting, and habitat stability must still be overcome for populations to become re-established.

KELLOGG, A. R. 1960. Mammals and how they live. Pages 13–15 *in* Wild animals of North America. Nat. Geog. Soc., Washington, D.C.

KILPATRICK, C. W., S. FORREST, AND T. W. CLARK. 1986. Estimating genetic variation in the black-footed ferret—a first attempt. Great Basin Nat. Mem. 8:145–149.

No genetic variation was observed for three proteins examined from saliva samples from 22 BFFs. No conclusions can be drawn, however, and suggestions are made for additional approaches.

KOFORD, C. B. 1958. Prairie dogs, whitefaces and blue grama. Wildl. Monogr. No. 3. 78 pp.

Classic discussion of *Cynomys* prairie communities based on fieldwork in Colorado. Details the ecology and trophic relations between prairie dogs and other members of the prairie, including BFF, and man and his domestics. Reference to BFF as obligate predator.

KOHN, S. 1978. Non-game wildlife—its acknowledgement and management. North Dakota Wildl. 40(9):6–7.

Nongame amenities are new in the public mind and have political and governmental support. North Dakota created one position in 1975 to manage nongame with emphasis on the BFF and prairie dog communities.

KURTÉN, B., AND E. ANDERSON. 1972. The sediments and fauna of Jaguar Cave: II—The fauna. Tebiwa 15:21–45.

Twelve BFF remains from Jaguar Cave, Idaho, fall outside the historic species range and date from 10,370 + 350 B.P. Suggested that the BFF, an Old World invader, is not as successful as *M. eversmanni* in Eurasia and now exists only as a relict population.

LANTZ, C. L. 1905. Kansas mammals in their relations to agriculture. Bull. Kansas State Agric. Coll. Expt. Sta. 129:331–404.

LAYCOCK, G. 1969. America's endangered wildlife. W.W. Norton and Co., New York. 226 pp.

Popular account of BFF within context of all endangered species.

LECHLEITNER, R. R. 1969. Wild mammals of Colorado: their appearance, habits, distribution, and abundance. Pruett Publ.Co., Boulder, Colorado. 254 pp.

Lists Colorado BFF sightings 1954–1969.

LENGKEEK, D. 1985. Black-footed ferret program in South Dakota. Pages 21.1–21.4 *in* S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.

The history of the BFF in the state is reviewed. Fifteen probable and one confirmed sighting were recorded between 1/1/80 and 1/1/84. The state goal has been to implement effective information and education programs.

LENTZ, R. J. 1964. Status of the black-footed ferret in southeastern Wyoming. Colorado State University Forest Recreation and Wildl. Cons. Dept. Unpublished manuscript.

An early survey for BFFs revealed only three reports (one of value). Three-quarters of respondents felt that BFFs should be protected, although few were familiar with the animal.

LEPPART, G. 1970. Black-footed ferret, a vanishing species. North Dakota Outdoors 32(11):18–20.

Overview article for public education but contains some misinformation. Illustrates BFF sign and requests sighting information.

LEWIS, J. C. 1973. Additional records of black-footed ferret in Oklahoma. Southwest. Nat. 18:350.

Three specimens noted: one undated, one from 1927, and a recent private mount donated to Oklahoma State University.

LEWIS, J. C., AND F. D. HASSIEN. 1973. Status of prairie dogs and surveys for black-footed ferrets in Oklahoma. Pages 60–75 *in* R. L. Linder and C. N. Hillman, eds., Proc. Black-footed Ferret and Prairie Dog Workshop, South Dakota State University, Brookings.

Sixty-three BFF reports may be authentic on the state's estimated 15,000 acres of prairie dogs. Despite intensive surveys 1971–1973, no BFFs were found in the Panhandle study area.

———. 1974. Status of prairie dogs and black-footed ferrets in Oklahoma. Proc. Oklahoma Acad. Sci. 54:20–24.

Concludes that BFFs are extinct or rare in the state—despite recent reports—because of lack of evidence during recent intensive surveys.

LIBASSI, P. T. 1974. Five queasy species. Sciences 14(7):23–29.

Popular discussion of status of BFF and different research approaches; also looks at Atlantic green turtle, sandhill crane, Bahaman swallowtail, and Apache trout.

LINDER, R. L. 1973. Black-footed ferret and prairie dog workshop summary. Pages 171–177 *in* R. L. Linder and C. N. Hillman, eds., Proc. Black-footed Ferret and Prairie Dog Workshop, South Dakota State University, Brookings.

Summarizes main workshop points, with a reminder that all activities should be conducted for the benefit of "the resource," namely the BFF and the prairie dog.

———. 1985. Recovery Team efforts. Pages 3.1–3.4 *in* S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.

Approved in June 1978, the Recovery Plan was based on available scientific data and presented broad flexible guidelines.

LINDER, R. L., M. E. ANDERSON, E. M. BRIGHAM, C. N. HILLMAN, D. L. LENGKEEK, A. L. LOVAAS, J. K. MC-DOWELL, AND W. W. PAINTER. 1978. Black-footed ferret recovery plan. U.S. Fish and Wildl. Serv. 145 pp.

Government plan outlining the objective of "maintaining at least one wild self-sustaining population of BFFs in each state within its former range." State-by-state implementation plan listing lead agencies, cooperators, activity priorities, and budgets. Includes letters of comment by plan reviewers.

LINDER, R. L., R. B. DAHLGREN, AND C. N. HILLMAN. 1972. Black-footed ferret-prairie dog interrelationships. Pages 22–37 in Symposium on Rare and Endangered Wildlife of the Southwestern United States, September 22–23, 1972, Albuquerque, New Mexico. New Mexico Dept. Game and Fish, Santa Fe.

South Dakota BFF population and habitat needed to sustain BFF. Purchase or easement of prairie dog colonies suggested as management practice. Results of landowner interviews on attitudes toward prairie dogs included.

LINDER, R. L., AND C. N. HILLMAN, eds. 1973. Proceedings of the Black-footed Ferret and Prairie Dog Workshop, Rapid City, South Dakota, 1973. South Dakota State University, Brookings. Offset. 208 pp.

Record of the first BFF-specific symposium (All articles are listed in this bibliography.) Excellent compilation of status of management, ecology, and politics of the rarest North America mustelid.

LIPSKE, M. 1981. Seldom-seen ferrets dress for privacy. Defenders, Dec.:11.

Brief description of BFF and its historic range. Includes a list of recent confirmed and probable sightings from 10 western states and two provinces provided by the U.S. Fish and Wildlife Service.

LOCK, R. A. 1973. Status of the black-footed ferret and black-tailed prairie dog in Nebraska. Pages 44–46 in R. L. Linder and C. N. Hillman, eds., Proc. Black-footed Ferret and Prairie Dog Workshop, South Dakota State University, Brookings.

History of Nebraska prairie dog control reviewed: the state has legislated annual control of colonies since 1903. Number of towns and acreages estimated from unsuccessful 1971 media blitz to locate BFFs.

LONG, C. A. 1965. The mammals of Wyoming. University of Kansas Publ. Mus. Nat. Hist. 14:493–758.

Brief technical synopsis with records of occurrence in Wyoming up to 1965; includes state range map.

LOVAAS, A. L. 1973. Prairie dogs and black-footed ferrets in the national parks. Pages 139–148 in R. L. Linder and C. N. Hillman, eds., Proc. Black-footed Ferret and Prairie Dog Workshop, South Dakota State University, Brookings.

No BFFs are known to exist on National Park Service lands, although past sightings are noted. No intensive surveys have been conducted. However, several parks have prairie dog populations that are controlled to curb emigration and expansion. Some prairie dog community research is being conducted; more is proposed.

McCANDLESS, A. D. 1908. A week in the saddle. Forest and Stream 71:329–330.

Reports a "new enemy"—minklike—decimating prairie dog towns in the Nebraska sandhills. Editor's note suggests it is the BFF.

McCLUNG, R. M. 1969. Black-footed ferret. Pages 102–104 in Lost wild America. William Morrow and Co., New York. 240 pp.

Brief synopsis of our knowledge of BFF: life history, search efforts, and poisoning controversy.

McNULTY, F. 1970. Reporter at large: controlling the prairie dog and protecting the black-footed ferret in South Dakota. New Yorker 46(June 13):40–90.

The BFF is used as a case study in a detailed popular article on the politics and history of wildlife killing by federal agencies.

———. 1971a. Must they die? The strange case of the prairie dog and the black-footed ferret. Doubleday, Garden City. 86 pp.

The controversial study of prairie dog control and BFF preservation in South Dakota 1964–1970. Skillful description of people and events resulting from USDI's dual poison and protect mandate.

———. 1971b. The black-footed ferret. Natl. Parks Conser. Mag. 45:9–13.

Overview article from a journalist who won acclaim for digging out the story about the plight of the BFF.

MADSON, J. 1968. Dark days in dog town—federal policy of poisoning prairie dogs, Audubon Mag. 70:38–41.

Critical review of dual role of Bureau of Sport Fisheries and Wildlife and the USDI in managing rodent control and endangered predator the BFF.

MANN, W. N. 1930. Wild animals in and out of the zoo. Smithsonian Sci. Ser. 6:287.

Captive BFF lifespan reported to be five years.

MARTIN, D. G. 1973. Ferret and prairie dog programs on Indian reservations. Pages 136–138 in R. L. Linder and C. N. Hillman, eds., Proc. Black-footed Ferret and Prairie Dog Workshop, South Dakota State University, Brookings.

Prairie dogs considered infestations on North and South Dakota Indian land, covering 70 thousand acres on seven reservations. Surveys conducted for BFF prior to control.

MARTIN, P. R. 1978. Black-footed ferret inventory and management development plan for southeastern Montana. Montana Fish Game Dept. 31 pp.

Positive circumstantial BFF evidence was found on 4 of 20 prairie dog towns surveyed in Montana in 1978, and one possible sighting was made. Recommendations for easements on critical habitat and future study are made.

MARTIN, S. J. 1983. Additional records of black-footed ferrets in Wyoming. Southwest. Nat. 28:95.

Reports finding of six BFF skulls in south central and southwestern Wyoming 1978–1979.

MARTIN, S. J., AND M. H. SCHROEDER. 1979. Black-footed ferret surveys on seven coal occurrence areas in southwestern and southcentral Wyoming, June 8 to September 25, 1978. Final rept. Wyoming State Office, BLM. 37 pp.

A single skull with teeth and mandible and some other bones were found in a survey of coal areas in Wyoming.

_____. 1980. Black-footed ferret surveys on seven coal occurrence areas in Wyoming, February-September, 1979. Final rept. Wyoming State Office, BLM. 39 pp.

Five BFF skulls were found in surveys of coal areas in Wyoming.

MASTERSON, L., AND J. M. CHILD. 1973. The black-footed ferret—predator in peril. Anim. Kingdom 76(2):9–11.

Reviews conflict of prairie dogs being on the "pest list" and BFFs on the endangered list. Mentions the 1080 ban and Patuxent Wildlife Research Center's capability to breed BFFs in captivity.

MEAD, J. R. 1885. Note on two Kansas mammals. Bull. Washburn Coll. Lab. Nat. Hist. 1:91–92.

Author relates observation of BFF in prairie dog colony while bison hunting north of Saline River in 1860.

MENKENS, G. E., JR., AND S. H. ANDERSON. 1985. Current prairie dog research. Pages 8.1–8.10 in S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.

Reviews recent literature on ecology and population biology of prairie dogs and describes research on effect of seismic activity on white-tailed prairie dogs.

MERRIAM, C. H. 1896. Synopsis of the weasels of North America. U.S. Biol. Surv. North Amer. Fauna No. 11. U.S. GPO, Washington, D.C. 33 pp.

Review of two subgenera Putorius (BFF) and Ictis (all other Mustela). Notes the similarity of BFF to Putorius eversmanni and P. putorius.

MERRICK, B. J. 1973. Problems and needs in black-footed ferret and prairie dog management. Pages 164–167 in R. L. Linder and C. N. Hillman, eds., Proc. Black-footed Ferret and Prairie Dog Workshop, South Dakota State University, Brookings.

Accuses agencies of mismanaging predator/rodent control programs. Lists a series of immediate research/ management goals including captive breeding and transplanting of populations.

MILLER, G. S. 1912. List of North American land mammals in the United States National Museum, 1911. Bull. U.S. Nat. Mus. 79:1–455.

BFF nomenclature determined as Mustela nigripes.

MILNE, L. J., AND M. MILNE. 1971. The cougar doesn't live here anymore. Prentice-Hall, Englewood Cliffs, New Jersey.

MOON, G. F. 1905. What have I got? Trappers World 1(5):4.

MOORS, P. J. 1950. Sexual dimorphism in the body size of mustelids (Carnivora): The roles of food habits and breeding systems. Oikos 34:147–158.

Sexual dimorphism in the mustelids is discussed.

MORE FERRETS FOUND—MAYBE. 1981 Sci. News 121:376.

News item on early research efforts on BFF population found in 1981. Photo.

MURIE, O. J. 1954. A field guide to animal tracks. Peterson field guide series 9. Houghton Mifflin, Boston. 375 pp.

Drawings of right front and hind tracks as well as scats from Garst's captive BFFs in Douglas, Wyoming.

NELSON, E. W. 1918. Smaller mammals of North America. Natl. Geog. Mag. 33:391–493.

This early popular account calls BFFs parasites in prairie dog colonies preying on the "hapless colonists." They are certain to disappear with the "inevitable extinction" of prairie dogs. Includes a color print of Louis Agassiz Fuertes' painting of the BFF.

NICE, J. 1982. Endangered species: A Wyoming town becomes ferret capital. Audubon 84(4):106–109.

Description of events following location of Meeteetse, Wyoming, BFF population in the fall of 1981.

_____. 1983. Long road to recovery. Natl. Wildl. 21:16–19.

A popular account of the primary actors in the second year of the Wyoming BFF program.

NOVILLA, M. N., J. W. CARPENTER, AND R. P. KWAPIEN. 1978. Dual infection of Siberian polecats with *Encephalitozoon cuniculi* and *Nepatozoon mustelis* n. sp. Paper presented at Symp. Comp. Path. Zoo Anim., Nat. Zool. Park, Washington, D.C., October 2–4.

Seven three-week old Siberian polecats died from dual infections. Encephalitozoonosis and hepatozoonosis may have ecological implications for the BFF.

OLIN, G. 1954. Animals of the southwest deserts. Southwest. Monuments Assoc. Pop. Ser. No. 8. Globe, Ariz. 112 pp.

OVER, W. H., AND E. P. CHURCHILL. 1941. Mammals of South Dakota. University South Dakota Mus. Zool., Brookings. 59 pp.

PETERSON, L. A., AND E. D. BERG. 1954. Black-footed ferrets used as ceremonial objects by Montana Indians. J. Mammal. 35:593–594.

Four Crow BFF relics located in Pryor, Montana. Skulls retained in skins.

PETTUS, D. 1985. Genetics of small populations. Pages 22.1–22.11 *in* S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.

Determining the level of genetic heterogeneity in BFFs should have high priority in recovery planning, since it is unknown whether they are subject to inbreeding depression, and critical management decisions rest on this information.

POWELL, R. A. 1979. Mustelid spacing patterns: variations on a theme by *Mustela*. Z. Tierpsychol. 50: 153–165.

Review of mustelid spacing patterns. Suggests BFF exhibits intrasexual territoriality.

———. 1982. Prairie dog coloniality and black-footed ferrets. Ecology 63:1967–1968.

Suggests that range overlap of BFF with that of the highly colonial black-tailed prairie dog caused the prairie dog adaptation for denser colonies. See response by Hoogland 1982.

POWELL, R. A., T. W. CLARK, L. RICHARDSON, AND S. C. FORREST. 1985. Black-footed ferret (*Mustela nigripes*) energy expenditure and prey requirements. Biol. Cons. 33:1–15.

An additive model to estimate BFF energy expenditure (for running, digging, investigating burrows, and thermoregulation) was based on field data from the Wyoming population and lab data from Siberian polecats. A BFF should eat 20 prairie dogs during the four winter months. More are needed by lactating females in summer. Implications for conservation are discussed.

PRAIRIE DOGS POISONED WITH "1080" ON PUBLIC LANDS IN SOUTH DAKOTA: the endangered species, black-footed ferret, also found there. 1965. Defenders Wildl. News 40(3):47.

News article on government use of 1080 on 500,000 acres of Bureau of Land Management and Bureau of Indian Affairs lands in response to stockmen's requests.

PROGULSKE, D. R. 1969. Observations of a penned, wild captured black-footed ferret. J. Mammal. 50:619–621.

Male BFF captured in South Dakota was held in an outdoor cage at a mink ranch for seven months. Activity patterns, behavior, condition, size, and feeding and killing behaviors were noted.

RANDALL, D. 1977. Only a few years left for Wyoming's ferrets. Defenders 52(2):113–116.

Review of Clark's Wyoming BFF search efforts and the state and federal policy problems associated with managing predators.

———. 1981. America's rarest mammal comes in from the cold. Defenders (Dec.):9–10.

The first popular account of the Meeteetse BFF find, describing some initial conservation studies.

———. 1983. Born-again ferrets. Defenders 58(4):2–6.

Popular account of the many interests affected by the discovery of BFFs in Meeteetse, Wyoming—ranchers, management agencies, biologists.

RICHARDSON, L., T. W. CLARK, S. C. FORREST, AND T. M. CAMPBELL III. 1985. Snowtracking as a method to search for and study the black-footed ferret. Pages 25.1–25.11 *in* S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.

Snowtracking is used on the Wyoming population to census BFFs and study winter ecology, specifically movements, activity area sizes, hunting behavior, intra- and interspecific interactions, and markings.

———. 1986. Black-footed ferret recovery: a discussion of some options and considerations. Great Basin Nat. Mem. 8:169–184.

A framework for recovery planning is presented since current numbers are insufficient to maintain long-term viability. Three options to increase BFF numbers include increasing habitat at their present location, finding more wild ferrets elsewhere, and directly manipulating the population through translocation and/or captive rearing—this last is strongly recommended, and accompanying considerations are presented.

ROBINSON, L. D. 1973. Black-footed ferret and prairie dog programs on Forest Service administered lands. Pages 125–133 *in* R. L. Linder and C. N. Hillman, eds., Proc. Black-footed Ferret and Prairie Dog Workshop, South Dakota State University, Brookings.

Prairie dog control on Forest Service units is accompanied by precontrol BFF surveys. The most serious management problem is determining presence of BFFs.

ROOSEVELT, T. 1893. The wilderness hunter; an account of the big game of the United States and its chase with horse, hound, and rifle. G. F. Putnam's Sons, New York. 472 pp.

Derisive but colorful report of the BFF "as blood-thirsty as the mink itself."

ROSE, D. J. 1973. History of prairie dogs in South Dakota. Pages 76–78 in R. L. Linder and C. N. Hillman, eds., Proc. Black-footed Ferret and Prairie Dog Workshop, South Dakota State University, Brookings.

Points out the role of federal lands as reservoirs for rodent pests. Rate of control is proportional to the health of the cattle market and drought.

ROSEBERRY, J. 1985. Wyoming BLM's role in black-footed ferret management. Pages 13.1–13.3 in S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.

The BLM receives and checks out BFF reports, participates in management meetings, and funds and sponsors research and publications, as well as conducting related activities such as prairie dog inventories and prairie dog habitat management plans.

RUSSELL, R. H. 1985. The black-footed ferret in Canada. Pages 20.1–20.2 in S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.

In 1983, the Committee on the Status of Endangered Wildlife in Canada formally designated the BFF as extirpated; the last specimen was collected in Saskatchewan in 1937. Recent possible sightings, however, led wildlife agencies to institute surveys in 1985.

SANZ, R., AND T. SHOEMAKER. 1984. The significance of trenching as a diagnostic characteristic of the black-footed ferret in white-tailed prairie dog colonies. Symposium on Issues in Technology and Management of Impacted Western Wildlife, Steamboat Springs, Colorado, November 1982.

In a brief survey in 1980, the lack of other evidence of BFF presence to corroborate 26 "trenches" led the authors to suggest that "trenches" may not be diagnostic of BFF presence on white-tailed prairie dog colonies.

SASKATCHEWAN DEPARTMENT OF TOURISM AND RENEW-ABLE RESOURCES. 1978. The status of the black-footed ferret Mustela nigripes (Audubon and Bachman) in Canada. Status repts. and evaluations., vol. 1.

SCHANTZ, V. S. 1943. Mrs. M. A. Maxwell, a pioneer mammalogist. J. Mammal. 24:464–466.

A BFF in the collection of an early woman naturalist in Colorado is verified by E. Coues.

SCHMIDLY, D. J. 1977. The mammals of trans-Pecos Texas. Texas A&M University Press, College Station. 25 pp.

SCHMITT, G. 1982. Black-footed ferrets. New Mexico Wildl. 27(3):16–17.

Overview of BFF's plight with reference to New Mexico. Lists seven counties where BFFs have been collected and an eighth credible sighting. Requests public input in a publicity campaign to locate BFFs.

SCHNEIDER, B. 1971. Montana's mystery mammal. Montana Outdoors 2(4):30–35.

Overview of history, identification, life history, behavior, and population status in Montana.

SCHREINER, K. 1973. Goals in endangered species management. Pages 4–10 in R. L. Linder and C. N. Hillman, eds., Proc. Black-footed Ferret and Prairie Dog Workshop, South Dakota State University, Brookings.

Written in reference to Endangered Species Conservation Act of 1969 but applies equally to the 1973 Endangered Species Act. Reviews legislated species conservation mandate and the nature of recovery plans and recovery teams.

SCHROEDER, M. H. 1985. U.S. Fish and Wildlife Service guidelines for black-footed ferret surveys. Pages 27.1–27 in S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.

A summary of the standardized "Black-footed ferret guidelines for compliance with the Endangered Species Act." Reviews the purpose of the guidelines, areas to be surveyed, methods and timing, kinds of data and training needed, coordination of survey methods, and procedures if BFFs are found.

SCHROEDER, M. H., AND S. J. MARTIN. 1982. Search for the black-footed ferret succeeds. Wyoming Wildl. XLVI(7):8–9.

Popular description of location of BFF population near Meeteetse, Wyoming, in the fall of 1981 and the subsequent telemetering of a male BFF.

SETON, E. T. 1929. Lives of game animals; an account of those land animals in America north of the Mexican border, which are considered "game," either because they have held the attention of sportsmen, or received the protection of law. Doubleday, Doran Co., Garden City, New York. 4 vol.

The first detailed popular account of BFF size and color, history, numbers, range and "haunts," breeding, habits, food, disposition, and "amusements," closing with a lament for its probable extinction from prairie dog extermination. Quotes many earlier authors.

SHEETS, R. G. 1970. Ecology of the black-footed ferret and the black-tailed prairie dog. Unpublished thesis, South Dakota State University, Brookings. 42 pp.

Eighteen excavated prairie dog burrows yielded 82 BFF scats, the contents of which were 86% prairie dog. A BFF-occupied prairie dog town had a significant decrease in prairie dog population. BFF diggings are compared to prairie dog diggings. BFF capture techniques are compared.

———. 1972. A trap for capturing black-footed ferrets. Amer. Midl. Nat. 88:461–462.

Photograph and description of successful use of tubular live-trap for capturing BFFs.

SHEETS, R. G., AND R. L. LINDER. 1969. Food habits of the black-footed ferret (Mustela nigripes) in South Dakota. Proc. South Dakota Acad. Sci. 48:58–61.

Food habits of a female BFF and four young were studied during summer 1968. Six prairie dog burrows were excavated and 56 BFF scats recovered. Prairie dog composed 82% of animal matter in the scats.

SHEETS, R. G., R. L. LINDER, AND R. B. DAHLGREN. 1972. Food habits of two litters of black-footed ferrets in South Dakota. Amer. Midl. Nat. 87:249–251.

Eighty-two scats recovered from 17 excavated black-tailed prairie dog burrows occupied by two female BFFs and their young were analyzed. Contents were primarily prairie dogs and mice.

SHELFORD, V. E. 1940. The smaller mammals of the Great Plains. Science 91:167–168.

Plains rodent population expanded at the turn of the century, and this created competition with stock. Refers to Merriam, who stated the BFF alone could hold prairie dogs in check. Suggests setting aside undisturbed ecosystems to study the life history and interactions of prairie species.

SHUFELDT, R. W. 1889. The carnivora. Forest and Stream 32:335.

States simply that Putorius nigripes, called the American or black-footed ferret, occurs in central regions east of the Rocky Mountains.

SHUMP, A. U., K. A. SHUMP, JR., G. A. HEIDT, AND R. J. AULERICH. 1974. A bibliography of Mustelids. Part 1: Ferrets and polecats. Michigan Agric. Expt. Sta. Journal Article No. 6977. 54 pp.

The first of a series of mustelid bibliographies, arranged by nine subject headings, covers literature 1900–1974.

SNOW, C. 1972. Black-footed ferret (Mustela nigripes). Habitat Manage. Ser. for Unique or Endangered Species. Tech. Note 168–2. BLM-USDI, Denver. 23 pp.

Semitechnical account of BFF ecology, with short bibliography.

SOPER, J. D. 1946. Mammals of the northern Great Plains along the international boundary in Canada. J. Mammal. 27:127–153.

Records of BFF specimens from southwestern Saskatchewan and southern Alberta.

———. 1961. Field data on the mammals of southern Saskatchewan. Canadian Field-Nat. 75:23–41.

Lists BFF as rare in southwestern Saskatchewan and southern Alberta. Cites eight documented occurrences of BFF ca 1907–1935, seven of these from Saskatchewan.

———. 1964. The mammals of Alberta. Hamly Press, Edmonton, Alberta. 402 pp.

SOUTH DAKOTA COOPERATIVE WILDLIFE RESEARCH UNIT, BROOKINGS. 1963– . Quarterly report, vol. 1– .

Quarterly reports include reports of continuing Unit project on BFF population located in Mellette County.

SOUTHWEST RESEARCH INSTITUTE. 1979. Training of dogs to detect black-footed ferrets. Final report.

Ten-month study to train dogs (Canis familiaris) to search for and discriminate BFF odors.

SPARKS, E. A. 1973. Prairie dogs and black-footed ferrets in Utah. Pages 102–104 in R. L. Linder and C. N. Hillman, eds., Proc. Black-footed Ferret and Prairie Dog Workshop, South Dakota State University, Brookings.

Only one BFF reported (1952) in Utah. Prairie dog populations have declined; Cynomys parvidens is endangered.

SPERRY, C. C. 1941. Food habits of the coyote. U.S. Fish Wildl. Serv. Wildl. Res. Bull. No. 4. 70 pp.

Analysis of 8,339 coyote (Canis latrans) stomach contents yielded 3 BFF remains.

STANLEY, A., AND P. YOUNG. 1954. Black-footed ferret (Mustela nigripes) in South Dakota. J. Mammal. 35:443.

Note on a road-killed female BFF in South Dakota in 1952 and deposition of skin and skeleton.

STRECKER, J. K. 1926. A checklist of the mammals of Texas, exclusive of the Sirenia and Cetacea. Baylor University Bull. 29(3):1–48.

Strickland, D. 1983. Ferret update. Wyoming Wildl. 47(3):4–6.

Account of Wyoming Game and Fish Department's activities in relation to the Meeteetse BFF find. Emphasis on administration; gives some biological information.

Stromberg, M. R., R. L. Rayburn, and T. W. Clark. 1981. Black-footed ferret prey requirements: an energy balance estimate. J. Wildl. Manage. 47:67–73.

This prey-use model estimates annual BFF energy needs for reproduction and determines ranges of prey numbers and BFF densities based on prey unit energy availability. Size of BFF preserve considered.

Stuart, J. E. B., and A. G. Christensen. 1973. The status of black-footed ferrets and prairie dogs in New Mexico. Pages 47–50 in R. L. Linder and C. N. Hillman, eds., Proc. Black-footed Ferret and Prairie Dog Workshop, South Dakota State University, Brookings.

Despite recent sightings, the status of BFFs in New Mexico is unknown. BFFs are often confused with bridled weasels (Mustela frenata neomexicana). Prairie dog numbers are increasing. Nongame protection legislation for endangered species is being considered.

Stuart, R. W. 1973. Needs in ferret and prairie dog management. Pages 149–153 in R. L. Linder and C. N. Hillman, eds., Proc. Black-footed Ferret and Prairie Dog Workshop, South Dakota State University, Brookings.

Proposes that best management for BFFs is management of prairie dogs by states through land acquisition and easements, with cost shared nationally.

Svendsen, G. E. 1982. Weasels. Pages 613–628 in J. A. Chapman and G. A. Feldhamer, eds., Wild mammals of North America: biology, management, and economics. Johns Hopkins University Press, Baltimore. 1,147 pp.

Synopsis of the ecology of two subgenera Putorius and Mustela. Claims that the BFF was useful to settlers because it inhibited prairie dog colony expansion. Notes that, because captive breeding trial failed, it appears that habitat preservation is the only way to save the species. However, he cites Hillman et al. 1979 as evidence that increasing prairie dog abundance does not increase BFF numbers.

Swenk, M. H. 1908. A preliminary review of the mammals of Nebraska. University of Nebraska Stud. Zool. Lab. 89:74.

Gives state records for the BFF, noting that it is not abundant there and is nearly always found near prairie dog towns. Locates the range, "Great Plains from North Dakota to northern Texas and west into the Rocky Mountains up to 10,000 feet."

Taylor, D. 1961. Notes on a recent collection of a black-footed ferret. Trans. Kansas Acad. Sci. 64:41.

Gives circumstances of collection and measurements of a male BFF caught by a "gloved hand" in Kansas in 1957.

Taylor, W. P., and W. B. Davis. 1947. The mammals of Texas. Bull. Texas Game, Fish, Oyster Comm. No. 27. 79 pp.

Brief account of characteristics and Texas distribution. Notes that BFF, now nearly extinct, is among the least known of more than 200 Texas mammals. Its "undoing" is its close association with prairie dogs.

Thorne, E. T., M. H. Schroeder, S. C. Forrest, T. M. Campbell III, L. Richardson, D. Biggins, L. R. Hanebury, D. Belitsky, and E. S. Williams. 1985. Capture, immobilization, and care of black-footed ferrets for research. Pages 9.1–9.8 in S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.

From August 1982 to September 1984, 59 BFFs were live-trapped and chemically immobilized without mortality or serious injury. Capture procedures, handling, and drugging techniques, along with precautions taken to prevent introduction of diseases are described.

Torres, J. R. 1973. The future of the black-footed ferret in Colorado. Pages 27–33 in R. L. Linder and C. N. Hillman, eds., Proc. Black-footed Ferret and Prairie Dog Workshop, South Dakota State University, Brookings.

Discusses history of BFF sightings (one high elevation), distribution of three prairie dog species in Colorado. Prairie dog inventory is planned with the goal of locating BFF habitat.

True, F. W. 1885a. The American ferret. Science 6: 549–550.

Introduces the BFF because "its rarity recommends it," notes the few specimens available, includes a drawing.

_____. 1885b. A black-footed ferret from Texas. Amer. Nat. 19:720.

BFF from Gainesville, Cooke County, Texas, was the second specimen recorded for the state. The first was from Abilene.

Truex, R. C., R. Belej, L. M. Ginsberg, and R. L. Hartman. 1974. Anatomy of the ferret heart: an animal model for cardiac research. Anat. Rec. 179:411–422.

Thirty-eight "black-footed ferret" hearts were studied with physiologic, microdissection, vascular injection, and histological methods. We question the species identification here.

TURNELL, J. 1985. The private landowner perspective. Pages 6.1-6.3 *in* S. H. Anderson and D. B. Inkley, Black-footed Ferret Workshop Proceedings, September 18-19, 1984, Laramie Wyoming. Wyoming Game Fish Dept.

A Meeteetse rancher talks about the impacts of having BFFs on his land and his participation in the BFF Advisory Team.

TURNER, R. W. 1974. Mammals of the Black Hills of South Dakota and Wyoming. University of Kansas Mus. Nat. Hist. Misc. Publ. No. 60. 178 pp.

States that the BFF is holding its own in western South Dakota but that land use and rodent control are changing distribution and abundance throughout the range. Only a few records are from the Black Hills. States that restocking of the state parks and national monuments could insure survival of BFFs.

TWO RARE PORTRAITS OF TWO RARE CREATURES; black-footed ferret and Attwater's prairie chicken. 1968. Natl. Wildl. 6(2):42–43.

Color photograph of a BFF.

TYLER, J. D. 1968. Distribution and vertebrate associates of the black-tailed prairie dog. Unpublished dissertation, Oklahoma State University, Stillwater. 85 pp.

USDI. 1965. Survival or surrender for endangered wildlife. Fish Wildl. Serv. Circ. No. 233. U.S. GPO, Washington, D.C. 15 pp.

USDI. Resource publications. U.S. Bur. Sport Fish. Wildl. Several reports are cited, as follows:

USDI. 1968. Rare and threatened fish and wildlife of the United States. No. 34, mixed paging, M-15.

Fact sheet on BFFs and other T&E species.

USDI. 1970. Rare and endangered wildlife. Page 112 *in* Wildlife research. No. 85.

Two females were caught and tagged in South Dakota, and their litters were observed in life history studies. Recent sightings extended BFF range 200 miles westward and eastward to within 35 miles of the Minnesota border. Sightings suggest a widely dispersed group of small, sparse populations.

USDI. 1971. Rare and endangered wildlife. Page 104 *in* Wildlife research. No. 94.

Seven BFFs were seen in western South Dakota in 1969, for a total of 30 individuals seen 54 times from 1966 through 1969 by Bureau of Sport Fisheries and Wildlife personnel. Summary of scat analysis. Suggests that BFFs diminish populations of *C. ludovicianus*.

USDI. 1972. Endangered species research. Page 106 *in* Wildlife research, 1971: problems, programs, progress. No. 111.

Western states survey prairie dog towns for BFFs. Discusses differences in colony characteristics of prairie dog species.

USDI. 1973. No. 94, p. 82. Rare and endangered species. Black-footed ferret.

USDI. 1973. No. 114, p. 289. Threatened wildlife of the United States.

USDI. 1969. The right to exist; a report on our endangered wildlife. U.S. Bur. Sport Fish. Wildl. U.S. GPO, Washington, D.C. 12 pp.

The BFF is an example of an endangered species whose habitat and prey base have been interrupted by human activities. Suggests preservation of dog towns.

USDI. 1975. Ferret-polecat research. *In* Fish and Wildlife News. Holiday issue, back page.

USDI. Fish and Wildlife Service. Patuxent Wildlife Research Center, Laurel, Maryland. Several unpublished reports are cited:

USDI. 1976a. Protection of the black-footed ferret during animal control operations. 4 pp.

Summarizes development of BFF precontrol surveys and zinc phosphide application guidelines for control use in Montana. Describes 1975–1976 Pine Ridge Indian Reservation and Buffalo Gap National Grassland surveys, where BFF sign was observed. Habitat preservation and management implication of control programs stated.

USDI. 1976b. Development of methods for monitoring black-footed ferret mobility. 1 p.

Plan to develop BFF telemetry techniques. Also mentions trip to Soviet Union to procure 48 Siberian polecats.

USDI. 1976c. Geographic distribution of the black-footed ferret. 3 pp.

Second consecutive year with no BFF sightings in South Dakota.

USDI. 1976d. Factors influencing reproduction of black-footed ferrets in confinement. 3 pp.

Work with captive BFFs and Siberian polecats, including birthing of five BFFs. None survived, apparently due to maternal neglect. Death of diabetic BFF.

USDI. 1977a. Factors influencing reproduction of black-footed ferrets in confinement. 3 pp.

Successful captive mating of one BFF pair. One live kit was produced but did not survive. Successful breeding of Siberian polecats and artificial ejaculation and insemination techniques.

USDI. 1977b. Geographic distribution of the black-footed ferret.

Review of the work on the Mellette County, South Dakota, BFF population. Recommends development of improved detection methods, extensive surveys, and habitat research.

USDI. 1977c. Development of methods for monitoring black-footed ferret mobility.

Experiments with telemetering Siberian polecats, with discussion of problems.

USDI. Fish and Wildlife Service. Endangered Species Technical Bulletin. Several issues reported news of the ferret:

USDI. 1977. Special report: captive breeding time slip-ping away for black-footed ferret. ESTB 2(11): 10–11.

Describes problems of two captive breeding pairs of BFFs, including age, health, and possible genetic problems. Researchers concerned about factors limiting re-production in the wild, such as small litter sizes, lack of prey diversity, canine distemper virus, and subterranean life.

USDI. 1978a. Black-footed ferret tied to prairie dog man-agement. ESTB 3(7):1,6.

Approval of recovery plan of FWS. Notes that prairie dog management is crucial, describes original range, decline, and outlines recommendations.

USDI. 1978b. Regional briefs, Region 6. ESTB 3(2):2.

Regional FWS personnel and recovery team coop-erate to train ferret-finding dogs in South Dakota.

USDI. 1978c. State report: Black-footed ferret, peregrine head New Mexico's agenda of endangered species program. ESTB 3(6):4–5.

New Mexico contracted for the training of two dogs to search for BFFs in towns slated for poison control, with plans to relocate any BFFs found.

USDI. 1979a. Endangered species: new challenge for the Navajo. ESTB 4(6):7–10.

The Navajos enacted a tribal endangered species act that includes the BFF. Several potential BFF areas exist on the Navajo Reservation. Some sign and one sighting from 1973 to 1974 search efforts led to continued surveys and publicity. Dog towns are surveyed prior to control efforts.

USDI. 1979b. Regional briefs, Region 6. ESTB 4(4):2–3.

Two FWS personnel and four dogs are trained to locate BFFs in Region 6.

USDI. 1979c. Regional briefs, Region 6. ESTB 4(11):2.

FWS awards contract for BFF search of 4,000 ha of prairie dog colonies with Labrador retrievers. Most loca-tions in South Dakota.

USDI. 1980a. Fisheries and wildlife research, 1980. Fish and Wildlife Service. U.S. GPO, Washington, D.C.

Highlights BFF survey activities in Wyoming, captive breeding and canine-distemper vaccine experiment at Patux-ent Wildlife Research Center, and mammary tumor and death of captive BFF.

USDI. 1980b. Ross A. Lock. Black-footed ferret, whooping crane, and bald eagle protected in Nebraska. ESTB 5(2):4–7.

Review of Nebraska's endangered species programs, including solicitation of BFF reports. No evidence has sur-faced since 1949.

USDI. 1981a. Regional briefs, Region 6. ESTB 6(7):3.

Several BFF sightings (one confirmed) reported in May and June 1981: Lyman and Putte counties, South Dakota; Uinta and Goshen counties, Wyoming; and Moffat County, Colorado.

USDI. 1981b. Regional briefs, Region 6. ESTB 6(8):3.

Report on questionnaire to determine current range of BFFs revealed 228 sightings. All states reported sightings since 1970 except Arizona.

USDI. 1981c. Regional briefs, Region 6. ESTB 6(10):3.

Dog-killed BFF collected near Meeteetse, Wyoming, 25 September 1981. First confirmed report since 27 March 1979, Dodd County, South Dakota, sighting.

USDI. 1981d. Regional briefs, Region 6. Black-footed ferret findings give biologists new hope. ESTB 6(12):1,6–7.

Successful short-term radio telemetry of male BFF at Meeteetse, Wyoming. Two photos.

USDI. 1982a. Fisheries and wildlife research, 1981. Fish and Wildlife Service. U.S. GPO, Washington, D.C. 114 pp.

Brief description of BFF killed in Meeteetse, Wyo-ming, in 1981. First Wyoming report since 1972 stock pond-drowned individual.

USDI. 1982b. Regional briefs, Region 6. ESTB 7(3).

T. Clark finds dead BFF on Meeteetse study area; an-other dead BFF found just north of Meeteetse.

USDI. 1982c. Regional briefs, Region 6. ESTB 7(4):6.

Wyoming Game and Fish Department appointed lead agency for Wyoming BFF recovery effort. Advisory team made up of representatives from Wyoming Game and Fish, Bureau of Land Management, Forest Service, Fish and Wildlife Service, University of Wyoming, and private landowner.

USDI. 1982d. Regional briefs, Region 6. ESTB 7(5).

Report of a "test" in South Dakota and Kansas during summer 1981 to stimulate reports of BFFs through publicity; of 26 reports, about 1/4 were deemed "probable."

USDI. 1982e. Regional briefs, Region 6. ESTB 7(6):5.

In addition to 9 BFFs reported by FWS biologists in November 1981, 11 more have been revealed by ISU/Biota snowtracking efforts. Fieldwork to continue.

USDI. 1982f. Regional briefs, Region 6. ESTB 7(12):6.

Two South Dakota State University students logged 650 hours searching for BFF sign in Mellette County, South Dakota, where last BFF was seen in 1972. No evidence of BFFs was found.

USDI. 1983a. Regional briefs, Region 6. ESTB 8(1).

D. Belitsky hired by Wyoming Game and Fish Department for BFF coordinator position.

USDI. 1983b. Regional briefs, Region 6. ESTB 8(2):8.

BFF Advisory Team meeting in December 1982 discusses future research and management for Meeteetse population; biologists continue winter surveys.

USDI. 1983c. Only known ferret population receives careful attention. ESTB 8(3):5–8.

Report of research activities by FWS and ISU/Biota since discovery of BFF 1 1/2 years earlier; history of BFFs; development of BFF Advisory Team; threats; and plans for recovery.

USDI. 1983d. Regional briefs, Region 6. ESTB 8(4).

Several documents being developed for management and recovery of BFF by Recovery Team, Region 6, BFF Advisory Team, and FWS Division of Research.

USDI. 1983e. Regional briefs, Region 6. ESTB 8(5):3.

Interim Management Guidelines Committee of BFF Advisory Team began drafting guidelines and announced operational protocol for researchers, photographers, and others in the BFF-occupied areas. Presentations were made in a town meeting in Meeteetse.

USDI. 1983f. Regional briefs, Region 6. ESTB 8(7):11.

Report of Recovery Team meeting in Rapid City with plans for revision of Recovery Plan.

USDI. 1983g. Regional briefs, Region 6. ESTB 8(8):9.

Report of BFF Advisory Team meeting agenda of increasing efforts to locate, capture, and mark BFFs while minimizing impact on the population; litter surveys ongoing.

USDI. 1983h. Regional briefs, Region 6. ESTB 8(9):6.

Max Schroeder leads workshops in Utah, Colorado, South Dakota, and Montana to educate field personnel in recognizing BFF sign and conducting surveys.

USDI. 1983i. Regional briefs, Region 6.

M. Schroeder hired as regional BFF specialist to coordinate research and management with all involved agencies.

USDI. 1984. Regional briefs, Region 6. ESTB 9(2):8.

Male BFF found east of Cody, Wyoming, in June 1983 subsequently identified as a European polecat.

VAN RIPER, W., AND R. J. NIEDRACH. 1946. Black-footed ferret. Nat. Hist. 55:466–467.

Five photos of BFFs with short article. Called a useful weasel because it lowers prairie dog populations and doesn't disturb humans.

VELICH, R. 1961. Notes on mammals from Nebraska and southwestern Iowa. J. Mammal. 42:92–94.

Author acquired mounted female BFF taken near Anselmo, Custer County, Nebraska, in 1938.

WAGGONER, D. 1965. Burying a weasel. Defenders Wildl. News 40(4):39.

Poem about the BFF reprinted from *Saturday Review*.

WARREN, E. R. 1906. Mammals of Colorado. Colo. Coll. Publ. Gen. Ser. No. 19 (Sci. Ser. 46):225–274.

Lists high elevation BFF collections from Teller and El Paso counties, Colorado.

_____. 1910. The mammals of Colorado, their habits and distribution. G. P. Putnam's Sons, New York. 2d ed., 1943, University of Oklahoma Press, Norman. 330 pp.

This early technical description includes skull characteristics and the Colorado distribution, including specimens from 3,075 m elevation and from west of the Continental Divide. Notes its association with prairie dogs and its "curious history of having been lost to science for many years" after its description by Audubon and Bachman.

_____. 1921. The small mammals of Colorado. Colorado Mount. Club Publ. No. 7. Denver. 31 pp.

WEAVER, J. L., AND T. W. CLARK. 1979. Mammals. Pages 63–76 *in* T. W. Clark and R. D. Dorn, eds., Rare and endangered vascular plants and vertebrates of Wyoming. Offset. 78 pp.

Synopsis of Wyoming records, habits, and habitat of BFFs. Map of locations.

WEMMER, C. 1985. Black-footed ferret management and research: views of a zoo biologist. Pages 31–31.10 *in* S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.

The major challenges of captive animal management are to simulate ecological and demographic factors vital to pre serving genetic variability and to minimize the risks of extinction to which small populations are prone.

YANONE, V. D. 1973. The black-footed ferret in Montana. Pages 41–44 *in* R. L. Linder and C. N. Hillman, eds., Proc. Black-footed Ferret and Prairie Dog Workshop, South Dakota State University, Brookings.

BFF status is unknown. Two road kills occurred 1952–1972. Most sightings from this century have been from the southeastern part of the state. The population has been reduced by (1) prairie dog control, (2) 1080 poisoning, (3) loss of habitat, and (4) road kills and shooting.

YOUNG, S. P. 1940. "Black boots" of the prairies. Amer. Forests 46:16–18.

Early popular article with photographs of a 1927 speci men from Montana. Interesting description of the contro versy over the BFFs existence during the late 1800s, which culminated in Coues' successful location of specimens. Good description of natural history, although there are some technical errors.

_____. 1946. Sketches of American wildlife. Monumental Press, Baltimore. 143 pp.

Provides good history of the documentation and controversy of the "black boots of the prairies" as well as basic life history information and six excellent 1929 photos (presumed to be the earliest taken of wild BFFs).

_____. 1954. Black-footed ferret (*Mustela nigripes*) in South Dakota. J. Mammal. 35:443.

A road kill in Perkins County, South Dakota, in October 1952 is recorded and deposition of the skin and skeleton is noted.

YOUNG, S. P., AND A. F. HALLORAN. 1952. Arizona speci mens of the black-footed ferret. J. Mammal. 33: 251.

Specimens from the most westerly portion of the species' range were collected in east central Arizona. One specimen collected in 1917 and a second in 1929.

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